Co-registration of eye movements and EEG during active vision

Dissertation

zur Erlangung des akademischen Grades Doctor rerum naturalium (Dr. rer. nat.)

im Fach Psychologie

eingereicht an der Mathematisch-Naturwissenschaftlichen Fakultät II

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Datum der Einreichung: 20.12.2013

Datum der Verteidigung: 25.04.2014

Abstract

Although natural vision involves an active sampling of the environment with several saccadic eye movements per second, electroencephalographic (EEG) correlates of visual cognition are predominantly recorded under artificial conditions of prolonged fixation. An alternative approach to EEG analysis, explored in the present thesis, is to time-lock the signal not to passive stimulations, but to the on- or offsets of naturally occurring eye movements, yielding saccade- and fixation-related potentials (SRPs/FRPs). Using simultaneous high-resolution eye-tracking (ET), this technique was applied in two contexts. The first part of the thesis (publications 1 & 2) investigated brain-electric correlates of microsaccades, small involuntary eye movements, which occur despite attempted fixation during traditional EEG paradigms. In a series of experiments, we show that SRPs from microsaccades present a significant, but normally hidden source of visuocortical potentials that is active in most trials and can confound the interpretation of stimulus-locked data under specific conditions. The second part of the thesis assessed the feasibility and utility of using FRPs in the study of natural reading. Publication 3 provides a review of artifact sources, low-level factors, and high-level influences determining the FRP waveform in free viewing and proposes methods to optimize signal quality. We then replicate the N400 word predictability effect, a cornerstone of neurolinguistic research, in left-to-right sentence reading and relate N400 amplitude to measures of fixation time. In publication 4, the FRP technique was combined with gaze-contingent display manipulations to investigate the depth of parafoveal preprocessing in fluent reading. Our results show that simultaneous recordings improve the understanding of electrophysiological data recorded during fixation, extend the EEG's methodological scope to naturalistic viewing scenarios, and help to integrate findings from EEG and ET research.

Keywords: EEG, eye-tracking, fixation-related potentials, free viewing, reading, microsaccade, saccadic eye movements

Zusammenfassung

Obwohl Blickbewegungen einen elementaren Bestandteil des natürlichen Sehens darstellen, werden hirnelektrische Korrelate der visuellen Verarbeitung im Elektroenzephalogramm (EEG) zumeist während passiver Stimulation des ruhenden Auges erfasst. Ein alternativer methodischer Zugang ist die Kopplung des EEG an Beginn oder Ende natürlich auftretender Augenbewegungen mit Hilfe simultanen, hochauflösenden Eye-Trackings (ET). Die resultierenden sakkaden- bzw. fixationskorrelierten Potentiale (SRPs/FRPs) wurden in zwei Forschungskontexten untersucht und angewendet. Der erste Teil der Arbeit (Publikation 1 & 2) befasst sich mit den elektrophysiologischen Korrelaten von Mikrosakkaden, unwillkürlichen Fixationsaugenbewegungen die auch während traditioneller EEG-Messungen auftreten. Es wird gezeigt, dass Mikrosakkaden trotz ihrer geringen Amplitude eine wesentliche, aber mit herkömmlichen Methoden kaum auszuschließende Quelle muskulärer und kortikaler Aktivität im EEG darstellen (mikrosakkadische SRPs), welche in der Mehrzahl experimenteller Durchgängen aktiv ist, und zur Fehlinterpretation reizgekoppelter Potentiale führen kann. Der zweite Teil der Arbeit demonstriert die Machbarkeit und Nützlichkeit von FRP-Analysen zur Untersuchung hirnelektrischer Prozesse beim Lesen. In Publikation 3 werden Einflüsse verschiedener Messartefakte sowie visuell-evozierter, motorischer und kognitiv modulierter Potentiale auf die FRP-Wellenform beschrieben und Methoden zur Signaloptimierung vorgeschlagen. Wir zeigen, dass sich im natürlichen Satzlesen der klassische N400 Wortvorhersagbarkeitseffekt reproduzieren und in Bezug zu Maßen der Fixationsdauer setzen lässt. In Publikation 4 wurde mittels FRPs das Ausmaß der parafovealen Wortverarbeitung bestimmt. Simultanes ET ist eine sinnvolle Ergänzung zur bestehenden EEG-Methodik, sowohl zur Kontrolle von Mikroaugenbewegungen, als auch zur Erforschung natürlichen Blickbewegungsverhaltens und Integration von Befunden der ET- und EEG-Forschung.

Schlagworte: EEG, Blickbewegungsregistrierung, fixations-gekoppelte Potentiale, Lesen, Mikrosakkade, sakkadische Augenbewegungen

Acknowledgements

This has been a long journey and there have been many people along the way that I wish to thank. First among these are my advisors Werner Sommer (at Humboldt University) and Reinhold Kliegl (at the University of Potsdam). I had the unusual privilege of having not one *Doktorvater*, but two, who always worked as a team and complemented each other perfectly. I wish to thank them for their caring attitude, their optimism and enthusiasm, their inspiring passion for sound science, and their extraordinary commitment to this project. They granted me unusual freedom and resources to pursue my research ideas, while advising and supporting me in every possible way.

The experiments reported in this thesis would not have been possible without many helping hands and heads. Ulrike Bunzenthal, Benthe Kornrumpf, Susann Meyberg, Anna Pajkert, Katharina Schäfer, Kerstin Unger, and Petra Schienmann helped to record much of the data. Thomas Pinkpank and Rainer Kniesche provided invaluable technical support over the years. Ulrich Reinacher taught me a lot of new MATLAB tricks, Kay-Michael Würzner improved the word lists of publication 4 with his corpus magic, and Nicole Düngel, Petra Köhler, and Cornelia Reggentin guided me through various bureaucratic labyrinths. I also wish to thank my other friends and colleagues at Humboldt University's Biological Psychology lab for their input and for the many inspiring discussions about the scientific and the not-so-scientific things in life. A special thanks in this regard goes to Annekathrin Schacht and Stefan Schinkel, as well as my former office-mates Sabrina Aristei and Chung-Shan Kao, with whom I shared not only a workspace, but plenty of good hours (and bad Ramen noodles).

I also greatly enjoyed the unique research environment at the University of Potsdam and the company of the smart and inexplicably modest people who work there. In particular, I wish to express my gratitude to Michael Dambacher, Jochen Laubrock, Konstantin Mergenthaler, Eike Richter, Sarah Risse, Martin Rolfs, Daniel Schad, Hans Trukenbrod, Christiane Wotschack and Matteo Valsecchi for sharing so much of their wisdom with me. Despite my (pseudo)random presence in Potsdam, they never complained when I suddenly appeared at their office doors and treated them as my personal panel of universal experts. Each visit was a source of new ideas and motivation.

Part of this work was done in the framework of DFG Research Group 868. This group proved to be a fertile ground for many productive exchanges, often during very enjoyable retreats. Chung-Shan, Hans, Martin, Michael, and my brother Felix helped greatly with their last-minute motivation and proof reading. My friends and family tolerated phases of mental absence and set me straight during periods of work-life imbalance. I am very grateful for that.

Finally, I wish to thank my parents for their unconditional support in every phase of my life.

List of original publications

1. Dimigen, O., Valsecchi, M., Sommer, W., & Kliegl, R. (2009). Human microsaccade-related visual brain responses. *Journal of Neuroscience*, *29*, 12321-12331 (*)
2. Valsecchi, M., Dimigen, O., Sommer, W., Kliegl, R., & Turatto, M. (2009). Microsaccadic inhibition and P300 enhancement in a visual oddball task. *Psychophysiology*, *46*, 635-644
3. Dimigen, O., Sommer, W., Hohlfeld, A., Jacobs, A. M., & Kliegl, R. (2011). Coregistration of eye movements and EEG in natural reading: Analyses and review. *Journal of Experimental Psychology: General*, *140*, 552-572
4. Dimigen, O., Kliegl, R., & Sommer, W. (2012). Trans-saccadic parafoveal preview benefits in fluent reading: A study with fixation-related brain potentials. *Neuroimage*, *62*, 381-393 (*)

(*) Article contains a supplement with additional materials, datasets, or analyses

Abbreviations

Used in the synopsis or the original publications.

µV	microvolt
ANOVA	analysis of variance
BESA	Brain-Electrical Source Analysis
cd	candela
CRA	corneoretinal artifact
CRT	cathode ray tube (monitor)
EEG	electroencephalogram
EMG	electromyogram
EOG	electrooculogram
ERP	event-related potential
ET	eye-tracking, eye-tracker
FEM	fixational eye movement
FD	fixation duration
FFD	first fixation duration
FRP	fixation-related potential
GD	gaze duration
GFP	global field power
ICA	independent component analysis
LMM	linear mixed model
M	mean
MLR	microsaccadic lambda response
MS	microsaccade
ms	millisecond
mSRP	microsaccade-related potential
MSEC	Multiple Source Eye Correction
N400, P300	signal components of the ERP
P1	first positive peak of the ERP, SRP, or FRP
PCA	principal component analysis
PSC	Potsdam Sentence Corpus
RT	reaction time
SD / SE	standard deviation / standard error of the mean
SFD	single fixation duration
SOA	stimulus onset asynchrony
SP	(saccadic) spike potential
SRP	saccade-related potential
VEP	visually-evoked potential

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Thesis summary

Introduction

Under natural conditions, visual attention and perception are closely linked to movements of the eyes. During most of our everyday activities – from reading a book (Rayner, 1998), to playing sports (Land & McLeod, 2000), driving a car (Kandil, Rotter, & Lappe, 2009; Land & Lee, 1994), or preparing a cup of tea (Land, Mennie, & Rusted, 1999) – we sample our visual surroundings with three or four saccadic eye movements per second – or more than 10,000 in any waking hour (Findlay & Gilchrist, 2003). In between these saccades, the uptake of new information occurs during brief, snapshot-like fixation pauses during which the eyes are relatively – although never completely – at rest. Normal vision therefore involves an active exploration of the visual environment in which the viewer seeks out task-relevant information in a stimulus or scene or the gaze is automatically attracted by salient events. A core challenge of experimental psychology and cognitive neuroscience is to understand the dynamics subserving this remarkable achievement to interact seamlessly with our visual world.

Much of our current understanding of the neural underpinnings of visual perception and visually-based cognition is owed to experiments that have studied human brain function non-invasively using event-related analyses of the scalp-recorded electroencephalogram (EEG), in particular in form of averaged event-related potentials (ERPs). However, because eye movements introduce strong measurement artifacts into EEG recordings, in the vast majority of these experiments, the process of seeing is studied under laboratory conditions that preclude any large movements of the eyes. Instead, participants are typically asked to hold their eyes still while isolated stimuli are flashed near the point of visual fixation. Obviously, by confining oneself to situations without (large) eye movements, the processes under investigation may differ in fundamental ways from the active process of real-world vision, as it is routinely studied in behavioral eye-tracking (ET) research.

An alternative approach to signal analysis, investigated in the present thesis, is to align the EEG to the beginning or end of naturally occurring eye movements, so that oculomotor actions, rather than passive stimulations, serve as the relevant signal time-locking points. Although the resulting *saccade-related potentials* (SRPs) and *fixation-related potentials* (FRPs) were first described many decades ago, a review of past studies suggests that still

surprisingly little is known about their properties, in particular when compared to the sizable body of research on traditional visually-evoked potentials (VEPs, Chiappa, 1997; Halliday, 1982; Tobimatsu & Celesia, 2006). Moreover, research on SRPs and FRPs, especially in situations involving more than a single saccade, has been hampered by methodological problems and a lack of precise eye movement recordings.

The overarching goal of the present thesis was to explore the feasibility, challenges, and benefits of combining EEG recordings with simultaneous ET at high spatiotemporal resolution. This co-registration technique was applied to investigate SRPs and FRPs in two research contexts: microsaccades and natural reading.

The first part of this thesis focused on the utility of co-registration in the context of traditional stimulus-response paradigms that require a steady fixation. Even under these controlled conditions, active vision continues at a miniature scale in the form of microsaccades (MSs) – tiny, involuntary jerks in eye position that occur about once or twice per second. While these miniature movements were once considered as just a "nervous tic" (Kowler & Steinman, 1980, p. 275), MSs have gained much prominence in recent years, based on findings that they may serve as indicators of a wide spectrum of neural and cognitive processes. In this work, we describe their electrophysiological correlates and demonstrate their relevance to conventional EEG/ERP data analysis (Original publication 1 & 2).

The second part of the thesis assessed the feasibility of co-registration during fluent, left-to-right reading, an activity where the contrast between the established laboratory procedures in reading research – the slow, tachistoscopic presentation of isolated words – and normal eye scanning behavior is obvious. We show that simultaneous recordings are a useful tool to study the process of word recognition under natural conditions (Original publication 3 & 4).

This thesis summary is structured as follows: The remainder of this first chapter provides a rather general overview on eye movements, electroencephalography, the associated recording procedures, and their limitations. This is followed by a brief summary of the SRP/FRP technique as an alternative to stimulus-locked analysis. The subsequent sections then provide the background on the two applications for co-registration – MSs and reading – and derive the specific research questions for each part of the thesis. While these sections are meant to facilitate the reading of the underlying articles, the technical details are covered in the *Original Publications*. After the introductory chapter, the main results of the

conducted studies are summarized. The final chapter constitutes an overall discussion and outlines perspectives for future applications of simultaneous recordings.

General background

Saccadic eye movements

To control input, the visual system is equipped with a toolbox of different eye movements, but the most frequent and salient type are the short, rapid, ballistic, and conjugate jerks known as saccades. Saccades are necessitated by the inhomogeneous organization of the retina that continues throughout its visual projections to the thalamus and the retinotopically organized areas of visual cortex. High acuity is limited to a small retinal section, the fovea centralis, which covers the central 1-2 degree around the point of fixation. Outside the fovea, resolution falls off steeply towards parafoveal (eccentricities from 2-5°) and peripheral (beyond 5°) regions of the visual field. The primary function of saccades therefore is to align the fovea with one salient or relevant portion of a scene after another.

Saccades are planned and triggered by an oculomotor network that includes the frontal and parietal cortex, basal ganglia, thalamus, superior colliculus, cerebellum, and brainstem reticular formation (Munoz & Everling, 2004; Munoz & Schall, 2003; Sparks, 2002). Three orthogonally aligned antagonistic pairs of extraocular muscles rotate the eye at peak velocities of up to hundreds of degrees per second. During a saccade, viewers can be considered as functionally blind, a fact that is demonstrated by the inability to see one's own eye movements in a mirror. This is a consequence of the motion blurring of the image sweeping across the retina at high velocities, visual backwards-masking by the new input at fixation onset, and, to a lesser extent, active mechanisms of saccadic suppression, which elevate visual thresholds during the movement (Matin, 1974; Ross, Morrone, Goldberg, & Burr, 2001). Inflow of new information is therefore restricted to the intervening fixation pauses, when a new volley of retinal outputs enters the visual system.

The active scanning process differs in several regards from passive or "pure" vision (Churchland et al., 1994). For example, during normal vision, the world is incessantly reprojected onto different retinotopic locations for brief periods of time, creating the need for compensatory mechanisms. Active vision also entails the need of selecting future saccade targets, the shifting of attention towards them, and the preparation of motor programs. At the same time, the coordinated operation of sensory and motor systems entails potential processing advantages (Schroeder, Wilson, Radman, Scharfman, &

Lakatos, 2010). For example, it allows for pre-saccadic enhancements of visual sensitivity at the saccade goal (Rolfs & Carrasco, 2012), the extrafoveal preprocessing of soon-to-be-fixated items (Henderson, Pollatsek, & Rayner, 1987; Schotter, Angele, & Rayner, 2012), as well as various forms of anticipation, evident, for example, in form of a predictive increase in cortical excitability at the time of fixation onset (e.g., Rajkai et al., 2008).

Eye-tracking

Eye-tracking allows the experimenter to capture the full complexity of oculomotor behavior, both in simplified settings and real-world situations. Among many techniques available for eye movement monitoring (Holmqvist et al., 2011), video-oculographic methods provide the most convenient option for a wide range of purposes. With these systems, gaze direction is derived from the position of the pupil center and usually also one or more corneal light reflexes within video images of the infrared-illuminated eyes. Once a participant has fixated several known locations on the observed plane, intermediate positions are interpolated to determine the point of regard. Current video-based trackers sample monocular or binocular gaze position at spatiotemporal resolutions of up to 0.01° and 2 kHz. The accuracy of calibrated (i.e., absolute) gaze position is on the order of half a degree under typical conditions. Once the eyes are tracked, saccade and fixation intervals are separated via position-, velocity-, and acceleration-criteria.

EEG & event-related potentials

Electroencephalography is among the most frequently used non-invasive methods to investigate brain correlates of low-level vision, visuospatial attention, and visually-based cognition. The EEG measures voltage fluctuations between electrode pairs attached to the scalp surface (Berger, 1929) that are believed to reflect summated post-synaptic currents of thousands of spatially adjacent, parallel-aligned and near-synchronously activated pyramidal cells in neocortex (Nunez, 2006). The major advantage of the EEG is that it provides a direct measure of electric activity of the underlying neural tissue with, in principle, unlimited temporal resolution. Methodological drawbacks are the inherently low spatial resolution and ambiguity of the signal. For example, whether or not the activity of a patch of layered neural tissue is scalp-recordable depends on its distance to the scalp surface, its spatial orientation, any distortions from the propagation through the intermediate tissue and skull, and the presence of canceling currents. This makes it difficult to infer from a voltage distribution at a limited number of electrodes the location, number, configuration, and relative strength of the signal-generating sources. However, voltage

topographies reveal at least the relative locations of the neural substrates involved in the processing of different stimuli.

Embedded in the spontaneous EEG are ERPs, small neural responses in the order of a few microvolts that are related to specific sensory, cognitive, or motor events and isolated from the background EEG by averaging over many events of the same type (Dawson, 1954; see also Rösler, 2005). The resulting ERP is essentially a three-dimensional signal (time × amplitude/polarity × electrode), consisting of an often fairly stereotyped sequence of positive and negative peaks or signal features ("components", e.g., P1, N1, P300) characterized by their polarity, latency, and topography. To decrease the impact of random pre-stimulus fluctuations, it is common to subtract the mean voltage per channel in a "neutral" baseline interval, usually immediately before the event of interest. Furthermore, the EEG is usually band-pass filtered to enhance the frequency bands carrying most of the physiological signal.

Any difference in waveforms elicited by stimuli belonging to different conditions can then be interpreted as differences in the average neural activity evoked by the presented items. Given a suitable design, this allows researchers to draw inferences even without a precise understanding of the brain circuitry engaged in each condition. An alternative to signal averaging in the time domain is to analyze event-related changes in the EEG's spectral power and oscillatory phase at a frequency of interest (time-frequency analysis, e.g., with wavelets; Herrmann, Grigutsch, & Busch, 2005); this can be achieved by band-pass filtering and rectifying the EEG epochs before or after averaging.

Ocular artifacts and passive vision

Because of their small amplitude relative to the spontaneous EEG, event-related EEG measures like the ERP are prone to contamination by environmental and biological artifacts. A strong source of the latter are eye movements, which distort the signal via three partially independent mechanisms: rotation of the eye balls, movements of the eye lids, and eye muscle activity (Berg & Scherg, 1991; Lins, Picton, Berg, & Scherg, 1993; Picton et al., 2000a, 2000b). Most likely due to a higher metabolic rate in the retina, there is a steady electrical gradient of 0.4–1 mV between the front (cornea) and back of the bulbus (Malmivuo & Plonsey, 1995; Young & Sheena, 1988). When the eye rotates, this corneoretinal dipole changes its spatial orientation and current flows to nearby electrodes via volume conduction, causing a step-like *corneoretinal artifact* (CRA). Similarly, *eyelid artifacts* arise whenever the lid slides over the positively charged cornea and connects it to the forehead (Berg & Scherg, 1994; Lins et al., 1993). This occurs during blinks and to a

lesser extent during upward or oblique saccades. A third and less well-known artifact is the saccadic *spike potential*, a brief biphasic spike at saccade onset believed to reflect the summated electrical activity of the extraocular muscles when they discharge in synchrony at movement onset (Balaban & Weinstein, 1985; Blinn, 1955; Keren, Yuval-Greenberg, & Deouell, 2010; Thickbroom & Mastaglia, 1986). The three mechanisms are active to varying degrees during different eye movements and combine to create complex spatiotemporal patterns of distortions across the scalp (Plöchl, Ossandón, & König, 2012). In case of the CRA and the eyelid artifact, distortions can be magnitudes larger than the ERP, especially at frontal electrodes.

The vast majority of laboratory setups therefore attempt to preclude eye movements by instructing participants to maintain fixation and refrain from blinking. For this purpose, a fixation mark is presented throughout the measurement or before each stimulation. To further discourage exploratory eye movements, visual stimuli are often presented at a small size and for durations below saccadic reaction time (< 150 ms). If multiple stimuli are shown in a trial, the common presentation mode is *rapid serial visual presentation* (RSVP), the successive tachistoscopic display of single items in foveal vision.

EOG and artifact correction

Compliance with fixation is traditionally controlled with the electrooculogram (EOG), the potential between pairs of facial electrodes placed on opposite sides of the bulbus. Because the EOG is a relatively pure measure of the CRA and its amplitude is approximately proportional to the change in the eye's angle of rotation, it can be used to monitor eye movements. Nevertheless, the EOG also picks up activity from other sources (EEG, muscle activity, ambient electrical noise) and its amplitude fluctuates over time with external factors (cf. Plöchl et al., 2012). Thus, even with optimal provisions (careful calibration, DC amplification, optimal preprocessing; Joyce, Gorodnitsky, King, & Kutas, 2002) the EOG's absolute gaze position accuracy is limited to 1°–2° and therefore vastly inferior to ET (Joyce et al., 2002; Malmivuo & Plonsey, 1995; Young & Sheena, 1988).

For the common case that artifact-contaminated trials – detected via the EOG – are too frequent to be rejected, a multitude of methods have been proposed to compensate for CRAs and eyelid-related artifacts (Croft & Barry, 2000; Delorme, Sejnowski, & Makeig, 2007; Ille, Berg, & Scherg, 2002). These methods make use of various mathematical techniques including linear regression (Gratton, Coles, & Donchin, 1983), primary component analysis (PCA), and other methods of blind source separation (Delorme et al., 2007; Klemm, Haueisen, & Ivanova, 2009). For example, independent component analysis

(ICA) decomposes the EEG into statistically maximally independent components to separate artifacts from brain activity. The correction method used and evaluated in the present thesis, *Multiple Source Eye Correction* (MSEC; Berg & Scherg, 1994; Ille et al., 2002) combines PCA, dipole modeling, and the recording of prototypical eye movement artifacts from each participant (see also *Summary of Results* and the details in Publication 3).

Interestingly, despite the sophistication of many of these algorithms, their use has been largely restricted to the compensation of blinks and accidental saccades under steady-fixation conditions. Their performance on heavily contaminated free viewing data has not yet been thoroughly evaluated.

Saccade- and fixation-related potentials

In this thesis, averaged potentials time-locked to saccade onset are called SRPs, while those aligned to their end are referred to as FRPs. Furthermore, our focus is on potentials accompanying or following the eye movement rather than those related to its planning (Becker, Hoehne, Iwase, & Kornhuber, 1972; Berchicci, Stella, Pitzalis, Spinelli, & Di Russo, 2012; Everling, Krappmann, & Flohr, 1996; Richards, 2003).

Despite a recent surge in interest in using SRPs and FRPs, they are not a new research topic. Rather, much of the conclusive work on these potentials is decades old. Post-saccadic brain activity was first observed during continuous EEG recordings in the form of sharp occipital waves, which tended to disappear during fixation, eye closure, and in darkness (Evans, 1951; Gastaut, 1951). Evans (1953) designated these potentials lambda waves and suggested that "abrupt changes in the retinal afferent impulses occur as the focus of macular vision shifts between areas showing contrast in brightness" (p. 73). While it was initially thought that this phenomenon was restricted to persons with an epileptic tendency, it was soon found that lambda waves were visible in the spontaneous EEG of most healthy subjects (Roth & Green, 1953; Shih & Thompson, 1998) and during various tasks that involve the scanning of patterned backgrounds (like watching a movie, Gastaut & Bert, 1954).

Much of the subsequent work over the next decades focused on the question of to which degree these potentials reflect visual afferences, central processes related to saccadic suppression or space constancy, or muscle and movement artifacts. Analyses of averaged SRPs (Gaarder, Krauskopf, Graf, Kropfl, & Armington, 1964) and FRPs (Rémond, Lesèvre, & Torres, 1965) revealed that the lambda "complex" (Rémond et al., 1965) consists of several phasic components appearing during and after the movement (Lesèvre & Rémond, 1972; Rémond et al., 1965). They also established a primarily visual origin: Lambda waves are

attenuated or absent in darkness or while scanning uniform fields (Ossandon, Helo, Montefusco-Siegmund, & Maldonado, 2010), vary with stimulus contrast (Armington, Gaarder, & Schick, 1967; Kazai & Yagi, 2005), correlate with the size of the response at the retina (Gaarder et al., 1964), tend to be delayed in patients with a demyelinating pathology of the optic nerve (Billings, 1989), and also follow the external tapping of the eye ball (Scott & Bickford, 1967). Furthermore, there is a strong resemblance between lambda waves and pattern-movement VEPs (Kurtzberg & Vaughan, 1973; Thickbroom, Knezevic, Carroll, & Mastaglia, 1991; see also Kazai & Yagi, 2003).

Nonetheless, the nature of the signal is still not fully resolved. One important property of lambda waves is that they grow with saccade size. Furthermore, the available evidence suggests that they consist of overlaid sub-components evoked at saccade onset and offset, which become temporally dissociated in the case of large and long-lasting saccades (Billings, 1989; Kurtzberg & Vaughan, 1977; Thickbroom et al., 1991; Yagi, 1979a, 1979b). For this reason, SRPs and FRPs emphasize different features of the same underlying lambda complex. Whether retinal inputs during the saccade (Scott & Bickford, 1969) are relevant for lambda wave generation is unknown. Finally, there is also evidence for non-visual contributions (e.g., Marton & Szirtes, 1982a; Skrandies & Laschke, 1997).

Despite an incomplete understanding of the basic waveform, SRPs and FRPs have been used to study perception and cognition in simplified saccade tasks and naturalistic settings (e.g., Barlow, 1971; Cooper et al., 1977; Kurtzberg & Vaughan, 1979; Marton, 1991; Yagi, 1995; see Publication 3 for additional references). However, many of these studies faced technical problems and data-analytic limitations, due to the lack of ocular artifact correction, the sparse recording from only a few (less contaminated) posterior electrodes, and the fact that only the EOG and no ET was available to estimate gaze position.

As a consequence, still relatively little is known about the properties of SRPs and FRPs or their modulation by cognitive processes in comparison to the exhaustive literature on visual ERPs. In the current thesis, we studied SRPs during attempted visual fixation and FRPs during natural reading. The reasons for choosing these applications and the specific research questions are detailed in the following.

Application 1: Microsaccades

The key assumption underlying the fixation requirement in EEG research is that steady fixation precludes oculomotor activity. Precise eye movement recordings prove this assumption wrong. It has long been known (e.g., Helmholtz, 1866) that even while fixating

a target, the eyes are never perfectly motionless, but produce seemingly erratic *fixational eye movements* (FEMs) at a small spatial scale. Figure 1.1b in Publication 1 shows an exemplary trajectory of monocular gaze position during two seconds of attempted fixation. These FEMs can be broken down into three components: Most fixation time is characterized by periods of *drift*, slow meandering eye movements that resemble a random walk (Engbert & Kliegl, 2004) during which the eyes move at velocities below 0.5° per second. Overlaid on the drift is a tiny high-frequency oscillation (30-100 Hz) with an amplitude of less than 1 arc-minute of visual angle. This so-called *microtremor* is too small to be reliably measured with current video-based ET systems and was therefore not considered in the present work. Most importantly, at typical baseline rates of 1-2 per second, drift intervals are interrupted by a *microsaccade* (MS), a rapid, jerk-like rotation of the eye with an amplitude that can range from a few minutes of arc to about one degree (Martinez-Conde, Macknik, & Hubel, 2004; Rolfs, 2009). [1]

In the context of the present thesis, two aspects of MSs are of particular importance. The first is that MSs correlate with at least some mental processes. The second is that MS may present a relevant signal source in human brain research. In the following, some general properties of MSs are reviewed first; afterwards, these specific aspects are discussed.

Microsaccades: Properties and functions. Fixational eye movements have been a research topic for almost a century (Rolfs, 2009). This research has been dominated by longstanding controversies about whether MSs – as their most salient component – serve any specific functional purpose in vision or whether they represent oculomotor noise (Kowler & Steinman, 1980; Steinman, Haddad, Skavenski, & Wyman, 1973) that is irrelevant or even detrimental for some visual functions (Collewijn & Kowler, 2008; Kagan, 2012; Martinez-

[1] Kinematic properties of MS vary according to the apparatus and criteria used for their detection. There is also disagreement about the range of movements that qualify as MS. Early studies, which attached optoelectric or electromagnetic contact lenses (search coils) directly to one eye – considered the gold standard of FEM measurement – reported considerably smaller amplitudes (typically below 0.2°) than recent ones. This led Collewijn and Kowler (2008, p.15) to conclude that video-based ET is of "borderline quality in relation to the traditional size range" of MS. Smaller amplitudes in earlier studies might be explained by the eye's additional inertia from the contact lens or the fact that subjects were well-trained in fixation (Cherici et al., 2012; Rolfs, 2009). A recent indirect comparison between search coil data from fixating monkeys and human video-based data indicates comparable amplitude distributions across species and techniques (Martinez-Conde et al., 2009). For the present work, this debate is in so far relevant as we must acknowledge the possibility that a subset of small MSs was missed with our setup.

Conde et al., 2009; Rolfs, 2009). Historically, there has also been a tendency to treat FEMs as a separate phenomenon from the larger and voluntary saccades occurring during normal vision (summed up as *macrosaccades* in the following). In recent years, however, this distinction has become more and more blurred (Kagan, 2012; Martinez-Conde et al., 2009; Rolfs, Kliegl, & Engbert, 2008), based on increasing evidence that micro- and macrosaccades share a wide range of characteristics.

Like macrosaccades, MSs are usually defined as binocular events that are at least partially conjugated in both eyes. Micro- and macrosaccades show not only similar kinematic profiles (Zuber, Stark, & Cook, 1965), but are controlled by overlapping neural circuits, at least at a subcortical level (Hafed & Krauzlis, 2012). Furthermore, both types of saccades are roughly comparable in their frequency of occurrence (between 1 to 4 Hz) and mutually interdependent in their rhythmicity (Rolfs, Laubrock, & Kliegl, 2006), hinting at a common generator (Otero-Millan, Troncoso, Macknik, Serrano-Pedraza, & Martinez-Conde, 2008; Rolfs et al., 2008). Movement amplitude per se also does not provide a clear-cut distinction, because trained participants can voluntarily produce small saccades in the amplitude range of MSs (Haddad & Steinman, 1973). Given these similarities, the most essential difference between MSs and macrosaccades is that the former occur while a person *attempts to fixate*.

Functions that have been tentatively assigned to MSs can be categorized into oculomotor error-correction (e.g., compensation of drift-induced fixation error) and perceptual functions that directly subserve visual processing (e.g., maintaining the visibility of stimuli by counteracting neuronal adaptation) and it is likely that FEMs fulfill both types of functions (Engbert & Kliegl, 2004). Interestingly, recent findings suggest that one purpose of MSs is to direct the region of highest acuity within the fovea to relevant parts of the fixated scene (Ko, Poletti, & Rucci, 2010; Poletti, Listorti, & Rucci, 2013). Again, this suggests that MSs serve the same core functions as macrosaccades, but on a miniature scale.

Systematic influences on FEMs. The first key aspect of MSs in the context of the present dissertation is that they are not just random events that are uniformly distributed over time. Instead, it has become clear over the last decade that their occurrence is correlated to at least some aspects of human attention and perception. After any sufficiently strong visual or auditory stimulation, the rate of MSs first drops below baseline, reaches a minimum after 100-200 ms, then usually rebounds to a temporarily higher peak rate between 200-400 ms (Engbert & Kliegl, 2003), and falls off again to the baseline rate. This stereotypical inhibition-rebound pattern is observed in response to both visual and

auditory sensations (Kanai, Muggleton, & Walsh, 2008; Rolfs, Engbert, & Kliegl, 2005; Yuval-Greenberg & Deouell, 2011).

Importantly, ET studies have established influences of various experimental variables on the rate, orientation, and amplitude of MSs during this inhibition–rebound sequence. Among these are low-level stimulus properties (e.g., contrast, shape, and modality; Engbert & Kliegl, 2003; Rolfs et al., 2005; Rolfs et al., 2008b; Valsecchi & Turatto, 2008) as well as attentional factors (the focus of exogenously and endogenously cued spatial attention; e.g., Engbert & Kliegl, 2003; Hafed & Clark, 2002; Kohama & Usui, 2002; Laubrock et al., 2010; Pastukhov & Braun, 2010). In addition, fixational instability exhibits individual differences, both within the population of healthy individuals (Cherici et al., 2012; Schulz, 1984) and between healthy individuals and clinical populations (Kapoula et al., 2013; Zhang et al., 2008; for a review see Martinez-Conde, 2006).

Oddball effects. Recent findings suggest that higher-level cognitive factors other than spatial attention can also influence MSs. In a series of studies, Valsecchi and colleagues demonstrated that microsaccadic inhibition is prolonged and the rebound is decreased whenever a participant encounters a so-called *oddball* stimulus, a rare and task-relevant item within a longer series of irrelevant standard items (Valsecchi, Betta, & Turatto, 2007; Valsecchi & Turatto, 2008). This shows that fixation behavior is sensitive to a process of stimulus evaluation that is abstracted from any physical properties of the stimulus.

The oddball task is also among the most widely used paradigms in EEG/ERP research. Rare and task-relevant stimuli are known to influence the amplitude of the P300 (Sutton, Braren, Zubin, & John, 1965), a late positive-polarity ERP component often regarded as an index of contextual updating in working memory (Donchin, 1981; Donchin & Coles, 1988; for a review see Polich, 2007). The classic finding is that the amplitude of the parietal P300 is largest for infrequent targets and smallest for frequent non-targets. Irrespective of target status or a-priori probability, P300 is also increased when a stimulus interrupts a sequence of stimuli belonging to the other category (e.g., a non-target following several targets, Jentzsch & Sommer, 2001). Notably, these P300 effects of target status, target frequency, and stimulus sequence reach a maximum in a similar time range (around 250-400 ms) as the oddball-induced microsaccadic inhibition. This raises the question of how these two phenomena relate to each other and whether MSs contribute in any way to the observed P300 effects.

Neural correlates in monkey. This leads to the second important aspect of MSs. Traditionally, FEMs have not been considered as a relevant factor in human EEG or

neuroimaging studies. Yet, there is much indirect and also some direct evidence suggesting that despite their minimal size, MSs could present a relevant source of scalp-recordable activity. Most data on the neurophysiological concomitants of MSs comes from recordings of single-unit activity or extracellular local field potentials in awake and fixating non-human primates. Such invasive recordings have shown that MSs modulate the rate of neuronal firing in areas throughout the visual pathway (Martinez-Conde, Otero-Millan, & Macknik, 2013), from the lateral geniculate nucleus (the thalamic relay center for visual information received from the retina; Martinez-Conde, Macknik, & Hubel, 2002; Reppas, Usrey, & Reid, 2002), to primary visual cortex (V1; e.g., Kagan, Gur, & Snodderly, 2008; Leopold & Logothetis, 1998; Martinez-Conde, Macknik, & Hubel, 2000; Martinez-Conde et al., 2002), extrastriate cortex (area MT: Bair & O'Keefe, 1998; area V4: Bosman, Womelsdorf, Desimone, & Fries, 2009; Herrington et al., 2009), and parietal areas related to visuomotor guidance (Herrington et al., 2009).

Most studies converge on the finding that in early areas like V1, effects of MSs are primarily post-saccadic, visually-driven, and excitatory responses generated by the MSs moving the receptive fields of neurons across the stationary stimulus (Martinez-Conde et al., 2013). The existence of visually-mediated suppression is more controversial (Kagan et al., 2008; Leopold & Logothetis, 1998). In the absence of a stimulus, extraretinal activity is also observed in one third of V1 neurons, but these effects are significantly weaker than the visual ones (Kagan et al., 2008). Finally, comparisons between the effects of MSs, small voluntary saccades, and passive stimulus motion indicate that neural responses in early visual areas are qualitatively similar in each case (Kagan et al., 2008). Thus, at the single-cell level in monkeys, MSs account for significant variation in neuronal activity.

Neural correlates in humans. The fact that large areas of visual cortex are activated near-synchronously by MSs (Martinez-Conde et al., 2013) indicates that their effects could also be scalp-recordable in humans. However, investigations into human electrophysiology are scarce and date back to three studies conducted in the 1960ies and 1970ies (Armington & Bloom, 1974; Armington et al., 1967; Gaarder et al., 1964) in which the authors recorded electrical responses from the retina and a single occipital EEG channel. FEMs were registered via light reflected by a mirror mounted on a contact lens or with the simple scleral reflection technique. Following fine eye movements, Gaarder et al. (1964) and Armington and colleagues (1967, 1974) observed a contrast-sensitive occipital potential that varied with the spatial frequency of the fixated pattern, increased with saccade amplitude, and correlated with the size of the response in the electro-retinogram. Around the same time, Yamazaki (1968) reported that MSs are preceded by a burst of electro-

myographic activity in the agonistic lateral rectus muscle, which also propagates to the EEG in form of a spike potential (Armington, 1978). Although some of these findings were prominently published at the time (Gaarder et al., 1964), they were rarely taken into account in the FEM or EEG literature until recently (see Publication 1 and Rolfs et al., 2009). Together with studies conducted in parallel to this dissertation (Carl, Acik, Konig, Engel, & Hipp, 2012; Keren et al., 2010; Tse, Baumgartner, & Greenlee, 2010; Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008), this early work will be revisited in the *General Discussion*.

Summary and research goals. In summary, behavioral research shows that MS properties can vary between conditions in many domains of research. At the same time, intracranial recordings in monkeys and early EEG studies converge to suggest that minimal retinal displacements may be sufficient to generate scalp-recordable visual transients in human observers. Given the ubiquity of MSs during any fixation task and the standard use of fixation instructions in cognitive neuroscience this raises the question whether MSs present an unrecognized source of cortical and muscle signal in the EEG.

The goal of the first part of the thesis was therefore to (1) establish the precise electrophysiological correlates of MSs in multi-channel EEG data and to (2) assess whether MSs influence the recorded brain activity in commonly used EEG/ERP paradigms. These questions were addressed in four co-registration experiments, published in two articles submitted as part of this dissertation (Publication 1 & 2).

Application 2: Reading

The second application of co-registration in the present thesis is in reading research. Reading is not only an essential cultural skill, but a complex mental task that involves – to some degree – about every visually-based process investigated in cognitive psychology. Eye movements in reading also relate in a direct way to what is probably the first definition of active vision: “So we must perceive in order to move, but must also move in order to perceive” (Gibson, 1979, p. 223).

Eye movements in reading. To comprehend a text, readers sample each line with a complex sequence of saccades, spanning a typical distance of 7–8 characters, and fixations, lasting for a mean of 200–250 ms. However, these average values vary widely as saccade targets and fixation durations are constantly adapted to momentary processing demands. The scanning process is also not strictly serial, but involves multiple fixations on some

words, the skipping of others, and occasional regressive saccades towards earlier parts of the text (Huey, 1908; Rayner, 1998).

With few exceptions, ET research on reading can be summarized in a straightforward way: Any aspect of the reading situation (e.g., screen contrast), reading material (e.g., length or lexical frequency of the fixated word), task-set (e.g., normal reading, proof-reading), or reading skill (e.g., dyslexia, speed reader) that increases processing difficulty also increases fixation duration or fixation probability. In addition, there is good evidence that these behavioral effects of processing difficulty are distributed across surrounding fixations – e.g., the processing of a difficult word can "spill-over" into the durations of subsequent fixations – although the exact conditions are still under debate (Kliegl, 2007; Kliegl, Nuthmann, & Engbert, 2006; Rayner, Pollatsek, Drieghe, Slattery, & Reichle, 2007).

Limitations of RSVP. Reading presents an obvious potential application for fixation-triggered EEG analysis, due to stark differences between normal behavior and the simplified presentation protocols used in the laboratory. While ET experiments on reading often approximate everyday reading situations, EEG studies on visual word recognition typically employ single-word presentations, foveal priming paradigms, or RSVP (Kutas & Federmeier, 2011; Kutas, Van Petten, & Kluender, 2006). With respect to sentence reading, this means that sentences are presented word-by-word in the screen center at a fixed pace.

The RSVP procedure has unquestionable benefits in that it minimizes ocular artifacts and reduces the overlap between neural responses evoked by successive word presentations. Nevertheless, it also presents a strong simplification – if not oversimplification – of the reading process: First, in RSVP, the reader has no control over the actual fixation target. Second, because there is no variation in saccadic landing positions, words always appear perfectly centered on the fovea. Third, the reader cannot control exposure time, adapt fixation durations to the local text difficulty, or precisely anticipate the moment when new input will enter the visual system. Fourth, at typical stimulus-onset asynchronies between 400-1000 ms, stimulation rates are slower than the pace of normal reading. Finally and by design, there is no parafoveal preprocessing of upcoming words.

This latter difference may be of special importance. On any given reading fixation, only about six to eight characters fall onto high-acuity foveal vision. McConkie and Rayner's (1975) classic experiments with gaze-contingent text masking techniques (e.g., moving-window paradigm) have shown that skilled readers also take up useful information from a wider perceptual span extending about 14-15 characters into the reading direction. When

this region of effective vision is reduced by masking peripheral letters, reading begins to slow down.

Reading and ecological validity. Taken together, these procedural differences raise the question of whether the complexities of reading are adequately captured by RSVP. An answer to this question is crucial for the validity of conclusions based on existing reports. Of course, the limitations of RSVP have been previously recognized and proposals have been made to render the procedure more natural. These include stimulation variants that are self-paced (using button presses; Ditman, Holcomb, & Kuperberg, 2007), present words at a reading-like pace (Dambacher et al., 2012), induce variation in the retinal position of the presented word (Hutzler, Braun, & Jacobs, 2008), or include parafoveal flanker words (Barber, Donamayor, Kutas, & Münte, 2010; Barber, Van der Meij, & Kutas, 2013). Furthermore, there have been several studies (Baccino & Manunta, 2005; Barlow, 1971; Burdette, Walrath, Gross, & Stern, 1986; Henderson, Luke, Schmidt, & Richards, 2013; Hutzler et al., 2007; Kretzschmar, Bornkessel-Schlesewsky, & Schlesewsky, 2009; Marton & Szirtes, 1988a, 1988b; Metzner, von der Malsburg, Vasishth, & Rösler, 2013; Simola, Holmqvist, & Lindgren, 2009) integrating eye movements and EEG in reading or reading-like situations in various ways (see the *Introduction* to Publication 3 for a review). Nevertheless, it is still largely unknown to what extent RSVP findings transfer to ecologically valid situations. This question can be addressed with FRPs.

Word predictability effects. Another benefit of combined recordings is their potential to compare, integrate, and reconcile the often disjunct bodies of empirical findings produced by ET and ERP studies. The dependent variables used in ET research, such as *first fixation duration* (the duration of the initial fixation on a word) or *gaze duration* (the cumulated duration of the first fixation and all immediate refixations) present only the endpoint of various sub-processes that jointly modulate fixation time. In contrast, FRPs can potentially reveal the dynamics of word recognition occurring within a single eye fixation.

A variable central to both ET and EEG studies on reading is word predictability, that is, the expectedness of a word from its local or global context. The predictability effect on the N400 component of the ERP (Kutas & Federmeier, 2011; Lau, Phillips, & Poeppel, 2008), a benchmark result in psycholinguistic research, describes the finding that less expected or semantically incongruous sentence continuations evoke a stronger negativity at

centroparietal scalp sites than expected and congruous words (Kutas & Hillyard, 1980).[2] Of course, there is also a corresponding effect on fixation durations: Low-predictable words are inspected longer than high-predictable words (Ehrlich & Rayner, 1981; Kliegl, Grabner, Rolfs, & Engbert, 2004; Kliegl et al., 2006). Given the importance of the predictability effect in both ET and ERP research on reading, we considered it as a suitable test case for a co-registration attempt under free viewing conditions.

Eye-mind link. An interesting question concerns the apparent mismatch between the relative timing of predictability effects in both measures (Rayner & Clifton, 2009; Sereno & Rayner, 2003). In RSVP, effects on the average N400 waveform only begin to develop around 200-250 ms after word onset and reach a maximum around 400 ms. Oculomotor effects, in contrast, are often already seen during the first fixation on a word (Rayner, Ashby, Pollatsek, & Reichle, 2004; Rayner, Binder, Ashby, & Pollatsek, 2001) and fixations as short as 140 ms have been described as being predictability-modulated (Sheridan & Reingold, 2012). The comparatively late N400 onset and peak are even more surprising when motor programming latencies are taken into account. It is usually assumed that in order for any cognitive process to influence fixation duration, it must do so before saccade programming enters the non-labile stage, that is, at an estimated latency of at least 80 ms prior to the end of the fixation (Findlay & Harris, 1984). By this logic, brain-electric effects of predictability should begin well before 200 ms (Hauk, Coutout, Holden, & Chen, 2012; Pulvermüller, Shtyrov, & Hauk, 2009).[3]

This "conundrum" (Rayner & Clifton, 2009) raises the question of whether predictability effects in both techniques reflect the same underlying process, or more generally, how the N400 relates to fixation behavior. However, existing comparisons have relied on separate

[2] More generally, N400 amplitude depends on the contextual support provided by the preceding items. This context can also consist of a single word: The N400 is also attenuated when a target word is preceded by a word that is semantically related to it (semantic priming) and in cases where a word is repeated (repetition priming).

[3] More rapid (<200 ms) influences of lexico-semantic and contextual variables on ERPs have been reported (e.g., Amsel, 2011; Dambacher, Rolfs, Göllner, Kliegl, & Jacobs, 2009; Dien, 2009; Hauk et al., 2012; Hauk, Davis, Ford, Pulvermüller, & Marslen-Wilson, 2006; Hauk & Pulvermüller, 2004; Sereno, Rayner, & Posner, 1998). However, these effects are small and, more importantly, so far temporally and topographically inconsistent across studies. Universally accepted evidence for effects prior to the N400 is still lacking.

recordings; considering the limitations of the RSVP paradigm, the discrepancy might be absent in fluent reading.

Models of reading. Finally, co-registration may help to constrain models of reading. Computational models of oculomotor control in reading (e.g., Reichle, 2011; Schad & Engbert, 2012) rank among the most successful attempts of recovering complex constellations of fixations because they provide plausible architectures and implementations of the dynamics between the recognition of words and the initiation of appropriately targeted saccades. However, models differ in core assumptions: Serial-attention-shift models (Reichle, 2011) assume that words of a sentence are recognized in a strictly serial order and that the initiation of the next saccadic motor program is tightly linked to the completion of specific sub-lexical or lexical processing stages. In contrast, according to processing-gradient models (Schad & Engbert, 2012), the recognition of several foveal and parafoveal words may occur at the same time during a fixation.

Preview benefit. One example where these models generate different predictions concerns the timing and depth of parafoveal preprocessing. As mentioned above, ET studies have used gaze-contingent techniques in order to determine the kind of information that is picked up from words before the eyes reach them. Specifically, in the *boundary paradigm* (Rayner, 1975) a target word is covered by a non-informative letter mask or a different word while it is still in parafoveal vision. Only during the incoming saccade, once the gaze crosses an invisible boundary, is the preview string replaced with the correct target word. The classical finding in this paradigm is that target words are fixated for shorter durations when a correct preview was provided. This is called the *preview benefit*. Because words are exchanged during saccadic suppression, readers often remain unaware of this manipulation.

This general benefit (also called *identity preview benefit*) suggests that many words are at least superficially processed by the time they enter foveal vision. Surprisingly, this property of normal reading has been considered only rarely in psycholinguistic ERP research and models of (isolated) word recognition (Barber & Kutas, 2007). One goal of the present work was therefore to provide a first description of how a correct preview influences the electrophysiological response to words.

Parafoveal semantic preprocessing. While it is clear that readers benefit from a correct as compared to an incorrect preview, a closely related question is whether they also profit from semantically related previews, that is, whether (and when) readers extract the *meaning* of words that are not yet fixated (Rayner, White, Kambe, Miller, & Liversedge,

2003). Serial attention shift models predict that semantic information from parafoveal content words (e.g., nouns, verbs) is usually not retrieved early enough to influence the current fixation duration, or if it is, the reader will subsequently try to skip the word (Rayner et al., 2003). Attentional gradient models, in contrast, allow semantic preprocessing, at least in principle (depending on parameter settings). The empirical evidence from ET studies on semantic parafoveal processing is ambiguous (*pro*: Hohenstein & Kliegl, in press; Hohenstein, Laubrock, & Kliegl, 2010; Schotter, 2013; Yan, Richter, Shu, & Kliegl, 2009, *contra*: Altarriba, Kambe, Pollatsek, & Rayner, 2001; Rayner, Balota, & Pollatsek, 1986). Likewise, there are conflicting results from ERP studies employing parafoveal flanker words (Barber et al., 2013) or simplified saccade tasks (Baccino & Manunta, 2005; Simola et al., 2009).

It is promising to investigate this question with FRPs for two reasons. First, although there is no consensus on the exact functional locus of the N400, this component is usually considered to be semantic in nature and has been linked to the retrieval (Kutas & Federmeier, 2000), inhibition (Debruille, 2007), and contextual integration (Holcomb, 1993) of meaning. So it could be the case that FRP measures are especially sensitive to semantic manipulations, possibly more so than eye movements. Second, FRPs should reveal the point in time when word meaning becomes available to the reader. Specifically, if two semantically associated words are read in succession, the onset of priming effects provides an upper bound for the latency of semantic access.

Summary and research goals. To summarize, the general aim of the second part of the thesis was to explore the feasibility and usefulness of co-registration for reading research. Specific goals were to replicate the word predictability effect in a realistic reading situation, to compare it to corresponding effects in oculomotor behavior, to study the impact of parafoveal vision on electrophysiological indices of word recognition, and to determine the timing and depth of parafoveal processing. From a methodological perspective, reading was also used as a proxy to understand the data-analytic challenges of FRP analysis during free vision and to evaluate procedures for data processing and artifact correction. These issues were addressed in two studies, published in two articles, submitted as part of this dissertation (Publication 3 & 4).

Summary of Results

Saccade-related potentials from microsaccades

(Dimigen, Valsecchi, Sommer, & Kliegl, 2009, *Journal of Neuroscience*)

Research questions & method

Publication 1 aimed to establish a description of surface potentials related to MS execution with state-of-the-art recording equipment. In two experiments, the participants' simple task was to fixate stationary stimuli as precisely as possible for intervals of 10 s. In the first experiment, the fixation target was placed on a high-contrast checkerboard. In the second experiment, it was displayed within medium-sized images of faces, a stimulus category frequently used in cognitive neuroscience. Whenever a participant's gaze deviated more than 2° from the target, the trial was repeated; as a consequence, participants were incentivized to fixate well. Microsaccades were detected as outliers in eye velocity using a previously published algorithm with an adaptive velocity threshold (Engbert & Kliegl, 2003; Engbert & Mergenthaler, 2006). The EEG was time-locked to MS onsets and also analyzed continuously as a function of instantaneous (sample-by-sample) eye velocity. Additionally, microsaccadic SRPs were compared to those of voluntary macrosaccades.

Summary of results

During prolonged fixation, MS were typically slightly below 0.3°, a visual angle corresponding to 1-2 printed letters when reading a book at a normal viewing distance. Despite their small size, each MS evoked sizable *microsaccade-related potentials* (mSRPs), consisting of three spatiotemporally distinct types of peri- and post-saccadic potentials.

Corneoretinal artifact. Like larger saccades, MS generate a CRA attributable to the change in orientation of the corneoretinal dipole. A comparison with macrosaccades confirmed previous findings that this artifact increases in proportion to saccade amplitude and extends these findings to the range of MSs. Because MSs rotate the bulbus by a fraction of a degree only, the resulting EOG artifact (3 μV for a 0.3° MS) is far below the rejection thresholds typically used in ERP studies to identify contaminated segments (20-150 μV). It follows that MSs at this scale cannot be detected at an acceptable rate of false alarms with traditional measures of fixation control.

Pre-saccadic potentials. Microsaccade onset was accompanied by a sharp spike potential whose dominant first half-wave peaked at movement onset (see also Yuval-Greenberg et al., 2008). In line with the notion that the spike reflects summated activity from the extraocular muscles – rather than an eye ball movement – the spike preceded the actual movement onset (cf., Yamazaki, 1968). Like CRAs, the spike potential has a maximum close to the eyes; however, the topography of its first half-wave is reversed with respect to that of CRAs, that is, a negativity is observed near the canthus towards which the bulbus is rotating. Furthermore, the spike potential's positive pole is not located at the opposite canthus, but at parietal electrodes. This difference is important: Because of its comparatively weak frontal lateralization, the spike is easily missed with EOG setups that reference one facial electrode against another. Instead, it is maximized in a "radial" montage (radial EOG) that measures the potential between facial and parietal electrodes (see also Keren et al., 2010). This opens the possibility to detect MSs via the muscle spike in the radial EOG.

Post-saccadic potentials. The key finding of Publication 1 concerned the post-saccadic wave form. Even the smallest MSs detectable with the current apparatus – of around 0.15° – evoked a sizable lambda complex, regardless of the fixated pattern (checkerboard or face). Its dominant feature is the *microsaccadic lambda response* (MLR), a P1 peak after about 105 ms that consists of a positive pole over occipital cortex and a weaker negative pole near the vertex. More generally, significant occipital responses were observed once the eye rotated faster than 22°/s. Using source modeling, MLR generators were consistently localized within the visual cortex.[4]

Comparisons between MSs and macrosaccades executed voluntarily on the same checkerboard revealed that both produced lambda responses with similar scalp distributions. While increasing saccade size from 0.3° to 4.5° led to a proportional increase in the size of the CRA, the spike potential and the MLR increased only moderately (although a later peak of the lambda complex grew substantially for larger saccades). Of course, the relationship between saccade size and lambda response is likely influenced by the specific pattern shifted across the retina. The general relationship between saccade size and lambda response amplitude is well established (Thickbroom et al., 1991; Yagi, 1979b) and

[4] Whether the MLR originated in striate cortex, early extrastriate cortex, or both could not be distinguished, since estimates varied with the type of model fit to the data (single dipole or bilateral mirror-symmetric dipoles). This ambiguity is a common problem when VEPs are modeled with discrete equivalent dipoles (e.g. Di Russo et al., 2005).

was also seen within the population of MSs. The key finding, however, is that minimal retinal displacements are sufficient to produce strong occipital responses in the same order of magnitude as those after larger gaze shifts.

A supplemental wavelet analysis showed that MSs also affect the frequency composition of the EEG. Replicating parallel work by Yuval-Greenberg et al. (2008), we found that in a wavelet-based time-frequency analysis, the sharp singularity of the spike potential translates to a broad-band spectral artifact that reaches far into the EEG's gamma band (> 25 Hz) and can therefore mimic an increase in the power of high-frequency oscillations. The spectral signature of the post-microsaccadic lambda complex was overall similar to that reported for visual ERPs (Makeig et al., 2002).

Impact of microsaccades on the event-related EEG

(Valsecchi, Dimigen, Kliegl, Sommer, & Turatto, 2009, *Psychophysiology*)
(Dimigen, Valsecchi, Sommer, & Kliegl, 2009, *Journal of Neuroscience*)

Research questions & method

The steady fixation experiments demonstrate that even during near-optimal fixation, MSs frequently generate what is most likely a volley of visual feed-forward activity caused by small shifts of the retinal image. The amplitude of these mSRPs was comparable to those of VEPs typically observed after flashing stimuli to the stationary eye. At the same time, our results show that MSs are unlikely to be detected with established methods of fixation control. Taken together, this implies that visuocortical potentials from MS might be frequently overlaid on stimulus-aligned EEG data with unknown consequences for signal analysis.

We tested this hypothesis by co-recording FEMs and EEG in the visual oddball task. As outlined in the *Introduction*, in this paradigm, participants are exposed to a long sequence of stimuli, some of which are task-relevant targets while the rest are non-targets that may be ignored. In the present case, participants maintained fixation, while equiluminant red or green discs briefly (100 ms) appeared once per second around a central fixation spot. In addition to stimulus relevance (target or non-target), the relative frequency of targets was varied between blocks (20, 50, or 80%). Participants silently counted the number of targets.

Summary of results

Traditional stimulus-locked ERP analyses replicated robust and independent effects of target status, target frequency, and the preceding stimulus sequence on P300 amplitude (Jentzsch & Sommer, 2001). At the same time, eye-tracking revealed that of over 15,000 analyzed trials, 86% contained at least one MS. The mSRP aligned to these MSs was again characterized by a small CRA, a spike potential, and a lambda complex. Interestingly, in this experiment, the MLR peak was followed by several cycles of a damped 10 Hz oscillation. With reference to similar occipital "ringing" responses occasionally observed after passive stimulation (Makeig et al., 2002), we refer to this phenomenon as *microsaccadic alpha ringing*. It indicates that under some circumstances, MSs can evoke an oscillation in the alpha range or trigger a phase reset of the ongoing alpha rhythm.

Sorting the single trials according to the latency of the first MS within each trial revealed substantial hidden contributions to the stimulus-locked EEG. Strong effects were found at electrodes near the occiput/inion (Oz/Iz) but also the vertex (Cz), i.e., the scalp sites corresponding to the positive and negative maxima of the MLR.

Condition effects on MSs. Behaviorally, MS probability showed the typical inhibition-rebound sequence. Importantly, this rate signature was cognitively modulated and differed systematically as a function of the relative frequency of targets in the block: the rebound to target stimuli was weaker and delayed in blocks in which targets were rare rather than frequent, and also weaker after sequence-breaking stimuli. The same factors affected mean P300 amplitude in the analysis time window (200-500 ms). Despite some differences in the interplay of the factors target status and target frequency in both measures, this shows that saccade generation and P300 amplitude are sensitive to largely the same manipulations in the oddball task and are jointly affected by what may be a common underlying process of stimulus evaluation (see the *Discussion* of Publication 2).

Effect on stimulus-locked ERPs. The condition-specific presence of MSs also has methodological consequences. Given that the number of MSs varied between conditions, we expected that mSRPs should contribute differentially to the condition ERP. Because the inhibition of MSs lasts about 200 ms, and the MLR needs more than 100 ms to peak, mSRPs should primarily affect late intervals of the recording epoch, more than 300 ms after stimulus onset. We were able to confirm this assumption indirectly by averaging ERPs separately for trials that did or did not contain at least one MS during the rebound

interval.[5] As expected, additional ERP contributions from MS-related signals tended to be stronger in conditions with a higher MS rate, relative to a MS-free baseline scenario. In addition to occipital distortions, the stronger rebound in trials with frequent targets meant that there was additional negativity at electrodes near the vertex in these trials. In other words, the presence of mSRPs contributed to the measured P300 effect at central electrodes (a relative positivity for infrequent as compared to frequent targets), and distorted the P300 effect topography, at least in late time windows.

How relevant are these distortions? Although the overlapping mSRPs were strong – i.e., larger than the P1 evoked by the onset of the oddball stimulus – their effect was attenuated in averaged data because of latency-jitter in MS occurrence. Furthermore, P300 oddball effects are among the largest cognitive effects known in ERP research. Thus, although the P300 topography was affected by MLRs, the resulting distortions were an order of magnitude smaller than the genuine P300 oddball effects. Furthermore, the P300 is often measured at centroparietal electrode Pz, which was less affected because of its location in-between the positive and negative pole of the MLR. This is also the reason why we did not consider the effect of mSRPs in Publication 2, in which we only used centroparietal electrodes to quantify P300 amplitude. Clearly, the classic P300 oddball effects are not an artifact of MSs; however, overlapping mSRPs explained some of the target frequency effect at central electrodes. Furthermore, mSRPs contributed significantly to overall EEG variance, especially at occipital electrodes.

Face classification experiment. In a supplementary face classification experiment, we tested whether these findings generalize to other tasks and stimulus configurations. With its easily discriminable stimuli, short stimulus durations (100 ms), and strict fixation instruction, the oddball experiment may have underestimated the magnitude of oculomotor activity in typical ERP experiments. The face experiment therefore used long presentations of complex pictorial stimuli and an emotion discrimination task that invited exploratory saccades. Furthermore, a fixation target was only presented before stimulus onset. Under these conditions, MSs as well as small exploratory saccades – and the resulting spike potentials and lambda waves – were present in virtually all trials (97%).

[5] This splitting of trials is artificial in the sense that it compares two extreme scenarios for this time window, a MS rate of zero versus a MS rate > 1. Rate differences of this magnitude are rarely encountered under realistic experimental conditions, and this analysis is therefore likely to overestimate the distortions produced by the more subtle effects typically reported in the literature.

In summary, our results show that active vision continues at a small scale during conventional ERP experiments. Fixational instability was found to be a source of brain signals in the majority of trials. In the oddball paradigm, MSs were modulated by the same factors as the P300. Although overlapping mSRPs cannot explain the extremely robust P300 effects in this paradigm, results suggest that they do influence stimulus-locked ERPs and the EEG spectrum, both in absolute terms and in a condition-specific manner.

Fixation-related potentials during natural reading

(Dimigen, Sommer, Hohlfeld, Jacobs, & Kliegl, 2011, *JEP:General*)

Research questions & method

The study described in Publication 3 pursued four objectives. The primary methodological goal was to understand the technical and data-analytical challenges of fixation-locked EEG recordings during free visual exploration and to evaluate the performance of an algorithm to compensate for CRAs. The second goal was to provide a description of the whole-scalp FRP waveform during natural reading and the low- and high-level factors modulating it. The third goal was to replicate the classic N400 word predictability effect and to assess whether its timing and topography translate to active reading. The final goal was to explore the interrelation between predictability effects in FRPs and those in different measures of fixation time.

In the experiment, participants silently read a corpus of 144 representative German sentences previously employed in ET (Kliegl et al., 2004; 2006) and stimulus-locked ERP studies (Dambacher, Kliegl, Hofmann, & Jacobs, 2006) on reading. Predictability effects were studied using naturally occurring variations in cloze probability. A word's cloze probability within a sentence is defined as the probability of correctly guessing it as the upcoming word after knowing the preceding sentence frame. To compensate for CRAs, the raw EEG was corrected with the surrogate variant of the MSEC method (Berg & Scherg, 1994)[6]

[6] Like PCA or ICA, surrogate MSEC is a spatial filter (Ille et al., 2002) that models the EEG as a linear combination of multiple scalp topographies, which define the spatial layouts of artifact and brain activity. Blinks and calibration saccades from each subject are subjected to a PCA to derive typical artifact topographies. Activity time courses for these artifact topographies are then estimated in the presence of a generic set of brain signal topographies (defined by a dipole model) and subtracted. The brain model reduces the subtraction of cerebral activity that is spatially correlated to artifacts.

The FRP was aligned to fixation onsets on content words and averaged according to the words' cloze probability. To describe the eye-brain relationship and the factors influencing the FRP, EEG amplitude in the N400 window was modeled at the level of individual fixations (analogous to "single-trial" analysis) with a linear mixed-effects model (Baayen, Davidson, & Bates, 2008; Kliegl, Masson, & Richter, 2010). The model controlled for influences of word and sentence properties in the quasi-experimental design but also included fixation duration or gaze duration as linear predictors of N400 amplitude.

Summary of results

Feasibility & data-analytic challenges. Concurrent ET required the handling of technical issues related to data acquisition and synchronization. Relevant problems were electromagnetic power line noise from the nearby ET as well as neck muscle inspersions and pressure artifacts resulting from head stabilization. These issues could be addressed by band-pass filtering the data (below 50 Hz), by careful adaptation of the participants seating position, and by foam-cushioning the forehead electrodes. Synchronization was achieved by means of shared trigger pulses sent to both recording systems. Regarding ocular artifacts, a key finding was that MSEC compensated for most of the CRA, with only weak residual distortions remaining (see Publication 3 for an in-depth evaluation of MSEC performance). In contrast, in its current implementation, the algorithm did not fully subtract the spike potential, because no prototypical topography for this topographically variable potential (Keren et al., 2010) was included in the definition of the spatial filter (cf. Ille et al., 2002, p. 123). Complete suppression of the spike potential remains an ongoing challenge (Hassler, Barreto, & Gruber, 2011; Keren et al., 2010; Plöchl et al., 2012).

Importantly, we found that the electrically independent eye position signal can serve as an external reference to objectively evaluate correction quality, for example by testing for correlations between gaze and EEG after correction. This criterion also revealed that two centroparietal midline electrodes were unaffected by CRAs during left-to-right reading, even without prior correction. Taken together, the results demonstrate that ocular artifacts are a tractable problem for FRP recordings in reading and show that ET is valuable to quantify and improve correction performance.

Influences on the waveform. While most previous SRP/FRP studies restricted data analysis to a few less contaminated electrodes, the high quality of ocular correction afforded a full topographic description of the FRP waveform. The reading FRP was dominated by the occipital lambda response peaking 104 ms after fixation onset. Importantly, the waveform was heavily influenced by overlapping potentials evoked by (a)

previous and following fixations and (b) the initial sentence presentation. Moreover, just as for MSs, the pre-, peri-, and post-saccadic waveform was affected by the size of the preceding saccade (Thickbroom et al., 1991; Yagi, 1979b). The exact retinal or extraretinal mechanisms underlying this effect are not understood.

Nonetheless, both issues, temporal overlap and the saccade size effect, are critical. Under normal conditions, changes in fixation duration and saccade amplitude are correlated to the cognitive variable of interest (e.g., predictability), leading to condition-specific distortions of the waveform and also causing problems in finding an unbiased baseline for FRP analysis. In control analyses, these issues were addressed with different approaches: (1) inclusion of saccade amplitude as a covariate in the linear mixed model, (2) repositioning of the FRP baseline to a neutral interval before trial onset, and (3) "post-hoc orthogonalization", i.e., the careful selection of matching or at least comparable fixation pools from each experimental condition. In particular, it was necessary to discard fixations occurring shortly after trial onset in order to avoid overlap with a long-lasting P300 elicited by the sentence presentation.

N400 replication. From a psycholinguistic perspective, the main result was a proof of concept that it is possible to recover the N400 predictability effect across the full scalp in a sentence reading situation. Despite large differences in the absolute wave shape of FRPs as compared to the ERPs in the reference dataset (Dambacher et al., 2006), distribution, size, duration, and peak latency of the N400 effect were remarkably similar. A possible exception to this general conclusion concerned the onset latency. Although conservative statistical testing produced an onset within the range usually observed in RSVP (Kutas et al., 2006), the onset was uncharacteristically "smeared out", meaning that marginally significant N400-like topographies were observed as early as 120-160 ms after the eyes had fixated the word. A likely explanation for this apparent forward-shift is the parafoveal preprocessing of the target word. This hypothesis was followed up on in Publication 4.

Eye-mind link. The experiment replicated previous studies in that unexpected words were fixated longer and more often. This oculomotor predictability effect was fast-acting and already influenced the initial fixation. The relationship between behavior and N400 was investigated using a variety of techniques, including the reverse time-locking of the EEG to the saccade leaving the target word, chronometric comparisons of the average N400 onset or peak latency with the distribution of fixation durations, and the joint modeling of N400 amplitude and fixation time. Overall, these analyses suggest that the N400 is more closely related to later oculomotor measures (gaze duration and refixation probability), but not first fixations. For example, across the range of cloze probability, predictability affected

N400 amplitude and refixation probability in a highly similar manner. Furthermore, we observed covariation between N400 amplitude and gaze duration that was not mediated by other word or sentence properties included in the model. This was not the case for the first fixation duration.

Despite their recording under the same conditions, the present experiment could not resolve the discrepancy in the relative timing of oculomotor and EEG measures previously inferred on the basis of separate recordings. For example, by the time the N400 effect peaked in averaged FRPs, in 75% of the cases the reader had already moved on to another word. Despite some indication for a more gradual N400 onset, the current study could therefore not establish a significant EEG effect which happened clearly before the first oculomotor effect and could pass as a plausible neural predecessor. However, the methodological insights gained in this experiment should facilitate the search for earlier FRP correlates of contextual fit (Dambacher et al., 2009) and lexical processing (Pulvermüller, Shtyrov, & Hauk, 2009).

In summary, the experiment demonstrated the feasibility of whole-scalp FRP analysis in active reading, yielded a replication of the signature N400 predictability effect, and provided a first indication that processing timelines are affected by differences in the experimental protocol.

FRPs and the depth of parafoveal preprocessing

(Dimigen, Kliegl, & Sommer, 2012, *Neuroimage*)

Research questions & method

After Publication 3 established the feasibility of the approach, Publication 4 built on these findings and applied FRPs to study the impact of parafoveal preprocessing on word recognition during reading. By definition, RSVP does not permit a preview of upcoming words and Publication 3 provided a first indication that this procedural difference is a cause for differences in the neural response to words. In natural reading, behavioral facilitations from a correct preview amount to 20-50 ms (Rayner et al., 2003) or roughly 10-25% of first fixation time. Given the size of this benefit, it would be surprising if there were not also a corresponding effect in the EEG. The first goal of Publication 4 was to establish an electrophysiological correlate of this identity preview benefit. The second goal was to investigate the controversial question whether preprocessing is restricted to sub-

lexical information (e.g., abstract letter codes, orthographic codes, or phonological codes; Rayner et al., 2003) or whether it extends to the level of meaning.

To maximize statistical power and to minimize the modulating effect of saccade amplitude on FRPs (see Publication 1 & 3) a simplified reading task was used. Participants read lists of unrelated German nouns from left to right and at the end of each trial indicated whether the name of an animal was contained in the list. For one word in each list, parafoveal information was manipulated. There were three experimental conditions. In boundary trials, preview words were unrelated (e.g., *sugar*), semantically related (e.g., *knife*), or identical (e.g., *blade*) to the target word seen at the same position after the saccade (*blade*). These trials permitted us to search for EEG correlates of behavioral preview benefits. In a separate set of parafoveal-on-foveal trials, preview and target word were simply shown at adjacent list positions (e.g., *knife blade*). This alternative presentation mode enabled us to test whether properties of the second word *n*+1 (*blade*) already exert an influence on behavior or EEG while the eyes still rest on the preceding word *n* (*knife*). At the same time, these trials served as a control for the word materials: even without any preprocessing, we should see robust effects of identity priming (in case of two identical words) and semantic priming (in case of two related words) on the N400 component once the reader foveates word *n*+1. Word materials were optimized on the basis of a preceding rating experiment.

Summary of results

General preview benefit. Fixation durations replicated the classic preview benefit in form of shorter fixations on correctly previewed rather than unrelated words. Importantly, the FRP showed a corresponding modulation. This effect, which we call *preview positivity*, was found between 200-280 ms as a relative occipito-temporal positivity for previewed words, affecting the falling flank of the FRP's N1 component. In addition, there was a trend for reduced (less negative) N400 amplitudes following correct previews. Control analyses ensured that (1) the peri-saccadic display change itself had no detrimental effect on the FRP (it produced no significant VEP), (2) the preview positivity was not a trivial consequence of the change in fixation duration or residual CRAs, and (3) the effect was independent of the participants' conscious awareness of the display manipulation. Instead, the results show that under fluent reading conditions, established EEG correlates of visual word recognition are altered by parafoveal preprocessing.

Parafoveal semantic processing. Importantly, neither in behavior nor in FRPs was there any evidence for a difference between unrelated and semantically related previews. Results are therefore not in support of the hypothesis that in the context of a word list reading task,

readers extract the meaning of not-yet-fixated words. Parafoveal-on-foveal trials allowed us to determine an upper bound for the latency at which semantic information became accessible. When neighboring words of similar meaning (e.g., *blade* and *knife*) were fixated in succession, the FRP to the first word was not influenced by the semantic relation. However, N400-like priming effects arose 160-200 ms after fixating the *second* word. Interestingly, this onset latency is below what is typically seen in experiments with semantic priming in the fovea (Rugg, 1985; Rugg, 1987). Like the preview benefit reported above, this forward-shift is consistent with the notion that sub-lexical properties of the second word (e.g., orthographic features) were already obtained during the preceding fixation – allowing a more rapid access to word meaning once the word entered the fovea. At a methodological level, these results demonstrate that gaze-contingent techniques can be combined with EEG recordings to study the time course and extent of parafoveal processing during active vision.

General Discussion

Although normal vision is fundamentally trans-saccadic, its brain-electric correlates are routinely studied under artificial conditions of enforced fixation. The present thesis explored the feasibility and benefits of combining EEG recordings with ET for the study of visually-based cognition. In all conducted experiments, spontaneous activity was aligned to the on- or offset of naturally occurring saccades, yielding saccade- and fixation-related potentials. The first part of this work focused on brain potentials elicited by involuntary eye movements in conventional EEG/ERP paradigms. In the second part, the fixation requirement was dropped in order to study word recognition under natural conditions and the data-analytic challenges that are associated with this approach. In the following, the two applications of co-registration are first discussed separately and future research perspectives are outlined for each one. This is followed by a methodologically oriented outlook and a conclusion.

Co-registration during fixation

The central assumption that motivates the ubiquitous fixation instruction in EEG and neuroimaging studies is that relevant oculomotor behavior – and the associated brain, muscle, and artifact activity – is effectively precluded by fixation. The current results challenge this notion by showing that MSs are a significant and usually hidden signal source contributing to the scalp-recorded EEG.

Microsaccade-related brain potentials. To characterize microsaccadic contributions to the EEG and EOG, involuntary eye movements were recorded during prolonged fixation of stationary stimuli and in two event-related paradigms. We found that just like much larger saccades, MSs produce a CRA, a muscle spike potential, and – given a fixated stimulus of sufficient size and contrast – a multi-peaked lambda complex, dominated by the microsaccadic lambda response arising from striate or extrastriate visual cortex. Importantly, whereas all three types of potentials increase with saccade size, they do so with different offsets and scaling factors. The size of the CRA is proportional to saccade size. In case of MSs, it is therefore too small to be reliably detected with conventional EOG-based methods of fixation control. Spike potential and lambda response, on the other hand, were evident even for the smallest MS measurable with the current ET hardware. The size of these potentials increases only moderately with saccade amplitude and it is within the same

order of magnitude for MSs and macrosaccades. In case of the lambda response, the relationship between saccade amplitude and EEG is probably also mediated by features of the fixated pattern and the resulting change in retinal stimulation generated by a MS of a given size (see *Future Directions* below).

Taken together, the present results show that brain potentials after minimal saccadic displacements are similar to those following larger saccades executed in isolation (Publication 1) or in reading (Publication 3 & 4). This conclusion is consistent with results from invasive recordings which have yielded little evidence for qualitative differences between the post-saccadic response to MSs and saccades in early visual areas (Kagan et al., 2008; but see also Tse et al., 2010).

A possible difference concerns pre-saccadic potentials. Gently rising, ramp-like potentials are seen before self-initiated saccades (Becker et al., 1972; Berchicci et al., 2012; Everling et al., 1996; Kurtzberg & Vaughan, 1982; Moster & Goldberg, 1990), and we saw at least some indication for one such potential, a parietal pre-saccadic positivity (e.g., Everling et al., 1996; Moster & Goldberg, 1990, but see also Berchicchi et al., 2012) before large reading saccades. In contrast, we observed no activity prior to MS, neither in Publication 1 nor in unpublished follow-up work (Dimigen, Werkle-Bergner, Meyberg, Kliegl, & Sommer, 2011; see also Armington, 1978). This lack of movement planning potentials might be explained by the fact that pre-motor signals from a 0.3° saccade are simply too weak to be recordable at the scalp. A likely alternative is that MSs are initiated without significant involvement of cortical structures (Hafed, 2011). This question could be addressed in the future by comparing the potentials preceding MSs and amplitude-matched voluntary saccades (Haddad & Steinman, 1973).

Relevance to event-related EEG studies. What are the practical consequences of these findings? Traditional thinking holds that the visually-driven ERP consists of a cascade of visual, cognitive, and response-related components, all triggered by what is typically a single stimulation at trial onset. Contrary to this belief, the current results show that visual cortex is engaged at least *twice* during a typical trial, once by the stimulus and at least once more by a MS. In both paradigms tested – a visual oddball and a face classification task – most trials (86% and 97%, respectively) contained significant additional brain activity from involuntary saccades. It follows that under circumstances in which a stimulus is of sufficient size and contrast, the EEG at occipital and fronto-central electrodes – the poles of the MLR – can be a mixture of potentials elicited by the initial presentation of the stimulus and potentials related to its renewed processing following a MSs.

This fact is most relevant if MS properties vary systematically between conditions. Here we followed up on findings by Valsecchi and colleagues (2007; 2008) suggesting that MSs are inhibited following the presentation of oddballs, a stimulus category known to enhance P300 amplitude. By independently manipulating stimulus frequency and task-relevance, we confirmed that MSs are affected by the same variables as the P300 (stimulus relevance, stimulus frequency, and stimulus sequence) and in a similar time window. Although the mechanisms by which cognition influences fixation behavior are not yet understood (see the *Discussion* of Publication 2 for some ideas), these results establish that the rate of MSs can be used as an additional peripheral measure to probe the brain's response to oddball stimuli.

At the same time, these findings raised the question of whether the P300 is distorted by mSRPs. In addition to influences on the absolute ERP waveform, we also found condition-specific topographical distortions generated by overlapping mSRPs. However, it was also clear that even at the most affected electrodes, they accounted for only a small fraction of P300 oddball effects, which rank among the largest cognitive effects in ERPs. Furthermore, P300 amplitude is often quantified at parietal electrode Pz, which was almost unaffected by mSRPs. This is also the reason why mSRPs played no role for the analyses in Publication 2.

General methodological implications. Whether or not undetected MSs will lead to inferential errors depends on several factors.[7] These include the size of the condition effect on MSs, the amplitude of the microsaccadic lambda complex, the electrode site and time window under investigation, and whether the EEG is analyzed in the time or frequency domain (Yuval-Greenberg et al., 2008). Because MSs are temporarily inhibited after the trial-initial stimulation, and their rate only begins to rebound after 200 ms, mSRPs mostly overlap with late parts of the ERP waveform. Furthermore, distortions from mSRPs are likely most relevant in settings where the variable under investigation produces small ERP effects and is expected to correlate strongly with MS occurrence. Examples for the latter are experiments which require the detection of visual stimuli near the perceptual threshold (which are more likely to be missed during MSs; Beeler, 1967; Herrington et al., 2009) or those that investigate perceptual alternations while viewing visually ambiguous stimuli (which are correlated to the occurrence of MSs, see *Future Directions* below).

[7] The fact that superimposed lambda waves reflect cortical activity rather than an "artifact" does not mean that they cannot lead to the misinterpretation of data. A hypothetical example would be the mislocalization of an ERP dipole source to a more occipital region in a condition with more MS.

The present findings add to a recent wave of studies suggesting that undetected MSs can lead to unwanted signal variance and data interpretation problems with several neuroimaging techniques. These include invasive recordings in non-human primates (Gur, Beylin, & Snodderly, 1997; Herrington et al., 2009), human electrocorticography in periorbital cortex (Kovach et al., 2011), the analysis of high-frequency oscillations in EEG (Reva & Aftanas, 2004; Yuval-Greenberg et al., 2008) and MEG (Carl et al., 2012), multifocal VEP recordings (Zhang et al., 2008), and functional magnetic resonance imaging (Tse et al., 2010).

Interestingly, however, a close reading of the literature reveals that the significance of FEMs as a hidden signal source was anticipated a long time ago, before the wide-spread use of event-related analyses in cognitive neuroscience. Following up on the results of what was likely the first co-registration study (Gaarder et al., 1964), Armington and colleagues concluded that "Responses to spontaneous eye movements appear as nonstimulus-locked fluctuation of the background against which signals are recorded and they therefore add to the variability. This method is designed to study these spontaneous responses, and eliminates this source of variability" and can therefore "result in an improved signal-to-noise ratio" (Armington, Gaarder, & Schick, 1967, p. 1539). The present findings support this conclusion.

Counteracting influences of microsaccades. A possible course of action is to reduce fixational instability as far as possible. Measures to achieve this include the use of strict fixation instructions (Steinman, Cunitz, Timberlake, & Herman, 1967), optimal fixation targets (McCamy, Najafian Jazi, Otero-Millan, Macknik, & Martinez-Conde, 2013; Thaler, Schutz, Goodale, & Gegenfurtner, 2013), and short stimulus durations (Dimigen et al., 2011b). Another way to minimize MS rate is to present two stimuli in short temporal succession (e.g., fixation display and picture) or to employ fast presentation rates in RSVP so that each stimulation triggers a renewed microsaccadic inhibition (Laubrock, Engbert, & Kliegl, 2008; Pastukhov & Braun, 2010). Finally, the lambda complex (but not the spike potential) could be attenuated by presenting low-contrast stimuli on uniform backgrounds.

Because none of these measures is likely to completely eliminate mSRPs, MS detection remains vital. The present results show that MSs cannot be identified with traditional EOG montages. Due to their relatively large spike potential, however, a reasonable detection performance is reached by looking for peaks in the high-pass filtered radial EOG, at least for MSs of more than 0.5° (as shown by Keren et al., 2010). In principle, this opens the door for a reanalysis of existing EEG datasets (without ET) in order to learn more about the

microsaccadic rate signature in paradigms that have not yet been scrutinized with ET. A disadvantage of the radial EOG method is that it does not provide accurate information about saccade size and orientation. Eye movement recordings therefore remain the best option to evaluate whether MSs affect the measurement. This can be tested in at most three steps: By sorting the raw EEG segments according to MS latency, by plotting basic MS properties for each condition, and by comparing trials with and without MSs in the time window of interest. These relatively simple checks could also be implemented into standard EEG software packages (Dimigen & Reinacher, 2012).

Another possibility is to correct for mSRPs mathematically. As shown in the reading experiments, CRAs from small saccades are largely eliminated with the MSEC method. For the case of the spike potential, which was not removed by MSEC, there is now converging evidence that it can be partially suppressed – although not fully eliminated – by using ICA (Hassler et al., 2011; Keren et al., 2010; Plöchl et al., 2012). The microsaccade lambda complex, on the other hand, represents cerebral activity that is topographically similar to VEPs and therefore not easily isolated in a distinct spatial ICA component. A more promising approach is to remove mSRPs via deconvolution methods designed to separate overlapping signals on the basis of known event latencies (here provided by the ET; see Dandekar, Privitera, Carney, & Klein, 2012 and the related discussion in Publication 3). The performance of ICA and deconvolution methods in isolating MS-related brain activity needs to be further evaluated.

Once mSRPs are detected and possibly also isolated, an alternative viewpoint is to treat them not as an artifact, but as an additional source of information available in most trials. This perspective is laid out in the following.

Future directions

Understanding low-level influences. A basic requirement for counteracting mSRPs or for exploiting their presence in future studies of cognition will be a better understanding of the mSRP waveform and the visual and non-visual processes contributing to it. One outstanding challenge in this regard is to model the mSRP as a function of the exact changes in foveal and peripheral retinal stimulation that are produced by a MS on a given stimulus pattern (e.g., by relating horizontal saccade size on a vertical grating to lambda response amplitude; see Armington et al., 1974 for a first attempt). Furthermore, EEG recordings in total darkness, while fixating a memorized target location (Mergenthaler, 2008), are needed to test whether extraretinal processes contribute to mSRPs.

EEG correlates of drift and microtremor. A further open question concerns the role of the other two types of FEMs. Can drift movements (of varying velocity and binocular coherence) and microtremor also generate synchronous activity measurable at the scalp? Drift-induced responses, which are sustained rather than burst-like, are found in a large subset of V1 neurons (Kagan et al., 2008) and recent studies have emphasized the importance of drift for the optimization of retinal inputs during free viewing (Kuang, Poletti, Victor, & Rucci, 2012). Although we did not observe any occipital activity following (monocular) eye velocities below 22°/s, the analyses of Publication 1 were not optimal to address this question, because the much slower drift (around 0.5°/s) was drowned in the high-frequency machine noise of the ET. With regards to a possible contribution of microtremor, it is noteworthy that Onton and Makeig (2009) have reported a high-frequency EEG oscillation near the ocular cavities which they attributed to muscle tremor. While it seems unlikely that drift or tremor constitute sources of EEG-recordable brain activity, co-registration studies could clarify this issue.

Relating neural and perceptual effects of MSs. Microsaccades can have pervasive perceptual consequences. They do not only correlate with changes in stimulus visibility (e.g., Martinez-Conde, Macknik, Troncoso, & Dyar, 2006) but also precede perceptual alternations while viewing visually ambiguous, bistable stimuli (e.g., Laubrock et al., 2008; van Dam & van Ee, 2006). A topic for future research is to relate brain potentials from MSs to their perceptual effects, for instance, the reappearance of a stimulus or a switch in its conscious percept. The most basic analysis would involve the comparison between percept-changing and percept-maintaining MSs. An interesting feature of MSs in this context is that they provide an exact time-locking point for an otherwise purely internal process – a change in visual awareness – that is normally difficult to capture with the EEG because of variability in manual response time.

Cognitive modulation of mSRPs? The reading experiments summarized above suggest that SRPs are sensitive to the same cognitive variables known to affect ERPs. Do mSRPs also reflect higher-level processing of the fixated stimulus? If so, does each MS that is made on a meaningful stimulus trigger a renewed and full-blown cascade of cognitively modulated, "endogenous" ERP components? Or is microsaccadic activity confined to early parts of the visual pathway? Preliminary evidence that mSRPs carry psychologically interesting information comes from Meyberg et al. (2013), who found that the scalp topography of the MLR reflects the observer's current focus of covert visuospatial attention – a property previously established for VEPs (Hillyard & Anllo-Vento, 1998).

Microsaccades and slow oscillations. A final question concerns the relationship between MSs and slow EEG oscillations. In Publication 1, MSs were followed by a "ringing" response consisting of several cycles of a 10 Hz oscillation. Can MSs reset the ongoing alpha cycle? Or is their occurrence itself time-locked to an underlying visual exploration rhythm in this frequency band? Several authors have put forward the idea that the rhythmic process of (micro)saccade generation is entrained to the phase of slow neuronal oscillations or vice versa (Bosman et al., 2009; Gaarder, 1967; Hafed & Ignashchenkova, 2013; Schroeder et al., 2010). Furthermore, there have been a few reports of pre- and post-saccadic alpha oscillations in the early SRP literature (Reiman, Korth, & Keidel, 1974; Rémond et al., 1965; Riggs, Merton, & Morton, 1974). Most notably, using simple analysis techniques available at the time, Gaarder et al. (1966) linked the occurrence of MSs to a specific phase of the EEG's occipital alpha cycle. In monkeys, Bosman et al. (2009) found that MS generation is coupled to a 3 Hz oscillation in visual cortex that jointly modulates neuronal excitability and MS generation. In the current experiments and follow-up work (Dimigen et al., 2011b), we observed post-microsaccadic alpha ringing, but no pre-saccadic activity in support of the hypothesis that MSs are coupled to slow EEG oscillations. However, this issue clearly merits further investigation.

Co-registration during reading

The second part of this thesis explored the benefits of co-recording eye movements and EEG during natural vision. As explained in the *Introduction*, the tachistoscopic stimulation procedures predominantly used in neurolinguistic research differ from the visual sampling process during fluent reading. Simultaneous recordings hold the promise to study reading in natural contexts and to combine the respective advantages of the ET and the EEG technique. In the long term, they may also help to integrate models of oculomotor control (which are inspired by ET data) with theories of single word recognition (which are inspired by ERP data; Barber & Kutas, 2007).

The present thesis aimed to take first steps in this respect. Our goal were to reproduce the N400 predictability effect in natural reading (as a proof of concept), to describe its relationship to fixation behavior, to investigate the general influence of parafoveal vision on the electrophysiological response to words, and to assess the depth to which upcoming words are processed. In two experiments, the EEG was aligned to fixation onsets while participants read sentences (Publication 3) or words lists (Publication 4) from left to right.

These experiments generated several main insights: First, the methodological problems associated with fixation-triggered EEG analysis during free viewing are manageable to an extent that permits the replication of established ERP effects. Second, while the typical topography of N400 effects generalizes to active reading, N400 onsets tend to be shifted forward. Third, despite indication for such a forward shift, co-registration did not resolve the discrepancy between the fastest effects in behavior and more delayed N400 modulations. Instead, the N400 was more closely related to later oculomotor measures. Fourth, the fact that normal reading allows for parafoveal preprocessing has a significant effect on the neural response to words once they enter foveal vision. Finally, there was no evidence that readers process the meaning of words before they fixate them in our word list reading paradigm. In the following, these main findings, the limitations of the present studies, and perspectives for future work are discussed. Conclusions regarding the technical feasibility of FRP recordings during free viewing are summarized in a separate *Methodological Outlook*.

N400 replication. A first basic question was whether classic psycholinguistic ERP effects can be replicated under active reading conditions. This is clearly the case. It was demonstrated here for the effects of contextual fit (Publication 3), repetition priming (Publication 4), and semantic priming (Publication 4) on the N400. In Publication 3, we found that the topography and size of the predictability effect were overall similar regardless of whether sentences were actively read or whether they were passively presented as in the RSVP study by Dambacher et al. (2006), who used the same materials but a slightly different selection of target words. The replication of this N400 effect in an ordinary reading situation with heterogeneous sentence materials and in- and outgoing saccades suggests the feasibility of fixation-based EEG analyses in reading. At the same time, it presents reassuring evidence regarding the ecological validity of data collected with RSVP.

These finding are in line with the results of early SRP studies on word recognition in reading-like situations conducted by Marton and colleagues in the 1980ies (Marton & Szirtes, 1988a, 1988b; Marton, Szirtes, & Breuer, 1985; Marton, Szirtes, Donauer, & Breuer, 1985) as well as a parallel work by Kretzschmar et al. (2009). Whereas all of these authors limited data analysis to a few less contaminated electrodes, the good performance of the ocular artifact method made it possible to reproduce N400 effects across the entire scalp in the present experiments. Furthermore, we could control for several of the confounding variables that can otherwise distort the waveform (see also the *Methodological Outlook*).

Differences to RSVP. While the N400's scalp distribution generalized to normal reading, this may not hold true for all aspects of the electrophysiological response. On the basis of studies with passive stimulation, the latency of the N400 has been described as remarkably constant in the visual domain (Kutas et al., 2006; Kutas & Federmeier, 2011). In contrast, we observed a tendency for the N400 to begin earlier in active reading. In Publication 3, the predictability effect was temporally "smeared out" with some weak, N400-like deviations (which did not survive correction for multiple comparisons) already seen within the first 200 ms. This shift was much clearer in Publication 4, where significant N400-like repetition priming effects arose very shortly (80-120 ms) after the fixation of a word that was repeated within the list. Although caution is necessary in the absence of a truly comparable (and preferably within-subject) comparison to RSVP, these results provide a first indication that the normal timeline of word recognition differs from what is commonly found with RSVP. The preview effects observed in the boundary paradigm, discussed further below, suggest that parafoveal preprocessing – rather than other properties of normal reading[8] – is the likely cause for this shift.

Eye-mind link. How do EEG correlates of reading relate to oculomotor effects? On the basis of separate recordings, researchers have argued for a mismatch between the latency of the N400 component – the primary and so far only robust index of lexicosemantic processing in psycholinguistic ERP research – and fixation durations in reading. In Publication 3, this "eye-mind link" was explored within the same dataset.

As expected, a word's predictability affected both fixation times and N400 amplitude. However, despite the tendency for a more gradual N400 onset, the basic temporal contingencies were the same as previously inferred from RSVP: the bulk of the electrophysiological effects occurred only after those in behavior. Several results indicate that the N400 was more closely related to the second (or even third) rather than the first fixation on a word. For example, N400 amplitude covaried with gaze duration, but not first fixation duration. Furthermore, there was a strong resemblance between the way in which predictability affected N400 amplitude and refixation probability. Taken together, these findings indicate that N400 amplitude is related to "lagged" effects in oculomotor behavior

[8] Fast presentation rates that approximate the speed of normal reading delay the N400 (Dambacher et al., 2012). Non-optimal fixation locations within words are probably also associated with costs rather than benefits. The effects of external versus internal pacing and active saccade preparation on the speed of word recognition are unknown.

that develop only after the first fixation or while the reader already fixates the next word (see Dambacher & Kliegl, 2007).

While the present results establish that direct comparisons between ET and EEG measures are possible, their co-registration could not yet resolve the discrepancy between the earliest effects in behavior and the delayed N400 effects. For a detailed chronometric analysis, follow-up studies should employ strong experimental manipulations of word predictability within constant sentence frames. If such an experiment is implemented with high statistical power, it should be possible to pinpoint the precise time lines of effects in behavior (via distributional analyses of fixation time) and FRPs and to search for electrophysiological effects of predictability prior to the N400 (Dambacher et al., 2009).

EEG effects of preview. Publication 4 focused on the question of how parafoveal vision influences word recognition. Although a large body of ET studies has shown that readers spend less time on parafoveally previewed words, influences of preview have rarely been considered in ERP research or in theories of (isolated) visual word recognition.

Using saccade-contingent display changes, it was possible to establish a neural correlate of the trans-saccadic benefit in behavior. When a correct rather than incorrect preview on a word had been available during the preceding fixation – the default case in normal reading – FRP morphology was markedly different over occipitotemporal brain regions from about 200 to 280 ms, while FRP components before 200 ms were unaffected.

What causes this change in the FRP waveform? The benefit from correct previews could be a compound effect that reflects facilitation at multiple levels (e.g., at the level of sub-letter visual features, orthographic, phonological, or lexical representations). The time course of this preview positivity, its onset over the left hemisphere, its topography, and estimated sources in lateral-occipital or occipitotemporal cortex are compatible with the prevailing view in ET research that much of the general preview benefit is due to some type of abstract orthographic information (e.g., letter identities), which is extracted parafoveally and retained across the saccade. The finding that the N400 also tends to be reduced after correct previews does not contradict this view, since this component is known to be attenuated by a host of factors that facilitate word recognition, including partial repetition priming (e.g., Holcomb & Grainger, 2006). It is also noteworthy that the preview positivity fell clearly within the first fixation on the word, which was significantly shorter after correct previews. Thus, facilitated processing in occipitotemporal cortex due to preview may cause the subsequent reduction in fixation time.

To better understand this effect, future studies could systematically vary the amount of preview (e.g., the number of correct letters) and the preview-target relationship (e.g., by changing the letter case peri-saccadically or by using phonologically related previews, Pollatsek, Lesch, Morris, & Rayner, 1992). They should also address the question whether the effect reflects only a benefit from a correct preview or also costs from the interrupted processing of the (wrong) preview string (Kliegl, Hohenstein, Yan, & McDonald, 2013). At a methodological level, these results demonstrate that FRPs can reveal changes in the efficiency of word recognition happening within a single eye fixation.

Parafoveal semantic processing. Finally, in Publication 4, we addressed the question whether in addition to sub-lexical information readers obtain semantic information from not-yet-fixated words. Processing-gradient models of oculomotor control (Schad & Engbert, 2012) assume that readers can, at least in principle, recognize multiple words in parallel and may therefore retrieve a word's meaning before looking at it. In contrast, serial attention shift models (Reichle, 2011) do not predict a very early access to semantic properties of not-yet fixated words. Here we took a multifaceted approach and investigated preprocessing effects in fixation durations and FRPs in the form of preview benefits and parafoveal-on-foveal effects.

Results were clear-cut: In neither measure and neither paradigm did we find evidence that readers process parafoveal words for meaning. The temporal resolution of FRPs made it possible to move beyond this simple null result and to trace the time course of semantic access. In parafoveal-on-foveal trials, semantic priming effects on the N400 revealed that word meaning was retrieved – i.e. started to interact with the meaning of the previous word – no later than 160-200 ms after the word was directly fixated. The absence of a parafoveal effect is therefore compatible with a serial account. It is more difficult to compare the observed time course of semantic processing against the predictions made by an attentional gradient model, due to the complex spatiotemporal dynamics of the attentional processing span in this model. The results seem compatible with this account if we assume that readers adapted their span from a broader to a narrower focus (Schad & Engbert, 2012) in the current list reading task.

It is possible, of course, that parafoveal semantic processing depends on contextual constraint which is absent in word lists. By showing lists of unrelated nouns, we deliberately precluded context-based predictions, the very process investigated in Publication 3. More generally, the answer to the question of semantic preprocessing may not be a simple yes or no; rather, the mixed results of previous studies can be taken as

evidence that the extraction of semantic features is highly dependent on the specifics of the reading situation. Properties of the sentence materials, the language being read (e.g., the closer association between graphic form and meaning in Chinese; Yan et al., 2009), and the words being presented as previews (associated or synonymous words; Schotter, 2013) may determine whether an effect is observed (Hohenstein & Kliegl, in press). A next step is therefore to use FRP recordings under conditions that are presumably optimal for parafoveal preprocessing, that is, with constraining sentences, strictly synonymous preview words, and possibly also in a non-alphabetic writing system (Yan et al., 2009). In any case, these results can be taken as evidence that co-registration is not an end in itself, but a viable method for hypothesis testing.

Taken together, the results show that with appropriate methodological considerations FRPs present a useful addition to the method spectrum of reading research. The brain dynamics of natural reading are probably best studied with a mix of techniques, including RSVP variants that capture some aspects of normal reading (Barber et al., 2011; Dambacher et al., 2012; Ditman et al., 2007), simplified saccade tasks (Baccino & Manunta, 2005; Marton, Szirtes, Donauer, & Breuer, 1985; Reichle, Tokowicz, Liu, & Perfetti, 2011; Simola et al., 2009), and simultaneous recordings during sentence and paragraph reading (Dimigen et al., 2011a; Henderson et al., 2013; Kretzschmar et al., 2009).

Future directions

Co-registration has many potential research applications in reading as well as other areas of research, such as visual search, face recognition, or scene perception. I briefly mention three examples.

Neural correlates of saccade targeting behavior. Co-registration provides an opportunity to investigate phenomena that cannot be studied with existing techniques. For example, about 10-15% of reading saccades move the eyes backward in the text, but little is known about what triggers these regressions. Short regressions are thought to reflect oculomotor error correction or word identification failures. Longer regressions are usually attributed to comprehension problems (Vitu, 2006), for example, after the encounter of words that force a reinterpretation of the sentence's syntactic structure (Frazier & Rayner, 1982). It is therefore promising to relate regressions of different length to established ERP correlates of syntactic processing, in particular the P600 component (cf., Dimigen, Sommer, & Kliegl, 2007). Similarly, around 15% of all content words are skipped by the reader (Rayner, 1998). By comparing skipping to no-skipping cases, FRPs permit the study of lexical

processing for words that are never fixated. As explained in the *Methodological Outlook*, these analyses will require a statistical model of the FRP waveform to partial out confounding effects of saccade length and direction.

Influences of preview on object, face, and scene perception. We found that preview significantly modulates the brain's response to words. However, extrafoveal processing is not exclusive to reading, but likely part of any real-world viewing situation, as also evidenced by faster reaction times to previewed objects (Henderson et al., 1987). The finding that saccade-contingent display manipulations are compatible with EEG recordings opens the door for a systematic study of preview effects on neural correlates of visual perception. One prediction is that mid-latency ERP components, such as the N1/N170 component evoked by objects, faces, or scenes, are attenuated by preview in a similar way as it was seen here for words.

Assessment of reading state or reading ability. Another prospect is to correlate SRPs or FRPs with differences in reading state and reading proficiency. For example, given the well-established attentional enhancements of VEP amplitude (Hillyard & Anllo-Vento, 1998), it may be possible to extract a continuous measure of the reader's attentional state from the peak amplitude of the lambda responses (Yagi, 1981) or other features of the waveform (e.g., the power spectrum). An exemplary topic for investigation could be mindless reading states during which the reader's thoughts wander off while the eyes continue to scan the text (Schad, Nuthmann, & Engbert, 2012). Long-term applications of co-registration could lie in the study of interindividual differences in reading speed and comprehension (Mossbridge et al., 2013) or the diagnosis of reading impairments.

Methodological Outlook

The cognitive neurosciences are seeing a transition from simple stimulus-response paradigms towards the study of complex behavior in natural contexts (Makeig et al., 2009; Schroeder et al., 2010). This goes along with a trend towards data-rich and multimodal recordings (e.g., Ritter & Villringer, 2006). Combined ET/EEG recordings are promising in both regards, provided that the associated methodological problems can be fully addressed. In the methodological review section of Publication 3, it is proposed that these challenges fall into four categories: (1) technical issues related to data acquisition and integration, (2) the compensation of the three types of ocular artifacts, (3) condition-specific differences in the degree of temporal overlap with the potentials evoked by other fixations, and (4) low-level influences on the neural response (see Table 0.1).

Technical issues. From a technical standpoint, the current results show that there are no relevant hardware or software obstacles for co-recording both time series. The increasing quality of head-free remote ET systems (which minimize electrical and physiological recording noise) and the availability of dedicated software for data synchronization and preprocessing (e.g., Dimigen & Reinacher, 2012) will further improve raw data quality and reduce the technical effort.

Table 0.1. Problems and solutions for simultaneous recordings during active vision

Problem	Solutions proposed
Technical	
line noise (50/60 Hz)	notch filtering [1], head-free remote ET [2],
artifacts from head stabilization	electrode foam cushions [3],
data synchronization	shared trigger pulses [4], D-A converter [3], software for data integration [5]
Ocular artifacts	
corneoretinal	MSEC [3,6], eye tracker-supported ICA [2],
spike potential	other ICA variants [e.g., 7,8,9]
eye-lid related	
Overlapping responses	
from preceding & following fixations	GLM-based deconvolution [10],
from other events (e.g., stimulus onset)	post-hoc fixation matching [11,12]
Low-level neural response variation	
due to:	"replay" conditions [13],
changes in saccade amplitude	post-hoc fixation matching [11,12],
saccade-induced changes in visual field	inclusion as covariate in linear model [3]

[1] Keren et al., 2010 [2] Plöchl et al., 2012 [3] Dimigen et al., 2011a [4] Baccino & Manunta, 2005 [5] Dimigen & Reinacher, 2012 [6] Dimigen et al., 2012 [7] Henderson et al., 2013 [8] Hutzler et al., 2007 [9] Ossandon et al., 2010 [10] Dandekar et al., 2012 [11] Luo et al., 2009 [12] Kamienkowski et al., 2012 [13] Burdette et al., 1986

Ocular artifacts. The current findings also suggest that – contrary to common belief – ocular artifacts are not the primary problem for EEG recordings during free viewing. First, correction may be omitted under specific circumstances, depending on electrode placement, filter settings, and the analyzed time window. Second, the MSEC spatial filter compensates very well for CRAs and eye lid artifacts. The spike potential was not properly suppressed with the current implementation of MSEC, but this can likely be achieved by using ICA in future studies (Keren et al., 2010; Plöchl et al., 2012). Third, gaze position provides a valuable reference signal to evaluate correction quality. It allows the experimenter to test whether residual artifacts remain in the data after correction (undercorrection) and whether genuine brain activity is distorted by the algorithm (overcorrection). Finally, as proposed in Publication 3, ET can also directly improve correction (see also Kierkels, Riani, Bergmans, & van Boxtel, 2007; Noureddin, Lawrence, & Birch, 2012; Plöchl et al., 2012) because it helps to distinguish between artifact components and brain signal components produced by methods of blind source separation (Plöchl et al., 2012; see Dimigen & Reinacher, 2012 for an implementation).

Overlap and low-level influences. The last two entries in Table 0.1 present more serious challenges: signal overlap and low-level response variation. In unconstrained viewing situations like reading or scene perception, the viewer determines the spatiotemporal sequence of fixations. This means that oculomotor behavior is almost inevitably correlated to the experimental condition. This quasi-experimental nature of normal vision creates the need to distinguish between direct and indirect effects of an experimental variable on the recorded neural activity.

Direct effects reflect differences in the brain's processing of the fixated item. Indirect effects, in contrast, are mediated by the correlated changes in oculomotor behavior. Consider, for example, a stimulus category or a task that produces larger saccades and shorter fixations. The former will lead to larger post-saccadic lambda responses and the latter to stronger temporal overlap with FRP components evoked by the next fixation. Although both factors will lead to condition differences in the measured brain activity, these differences are in no way indicative of the specific neural circuitry engaged by the item or task under investigation. Rather, they are spurious manifestations of the oculomotor effects.[9]

[9] Another indirect effect is the genuine but topographically misleading occipital activity produced by MSs.

Based on the present results and previous findings there is little doubt that the largest cognitive ERP effects (e.g., N400, P300) can be reproduced in free viewing. This probably holds true even if the issues in Table 0.1 are not or not fully addressed (Cooper et al., 1977). Yet, the logic of the ERP method rests on the ability to interpret *any* statistically significant difference in the recorded waveforms, irrespective of its size. In order to develop FRPs into a reliable tool for vision research – and with regard to practical applications in clinical diagnostics (Billings, 1989; Jagla, Jergelova, & Riecansky, 2007; Kurtzberg & Vaughan, 1979; Marton & Szirtes, 1982b), human factors research (Daimoto et al., 2007; Kazai, Abe, & Yagi, 2005; Yagi, Imanishi, Konishi, Akashi, & Kanaya, 1998), or consumer studies – the inherent confound between behavior and FRP must be resolved.

Critical covariates. In the present work we have identified several covariates that need to be considered: the duration of the previous and subsequent fixation, the latency of the current fixation relative to trial onset, and the amplitude of the preceding saccade. There are likely more. In normal vision, retinal inputs vary considerably as a function of the inspected stimulus region. As outlined in the introduction, FRPs are essentially an extraordinarily complex type of VEP and many of the stimulation parameters known to influence VEPs (Chiappa, 1997; Halliday, 1982) are therefore also expected to affect FRPs. One such influence is probably the luminance contrast between stimulus regions that fall onto the fovea on successive fixations (Kazai & Yagi, 2005; Lesèvre & Rémond, 1972; Ossandon et al., 2010; Rémond et al., 1965). More generally, it may be necessary to model the saccade-induced changes in retinal stimulation for the entire visual field (foveal and peripheral) in order to fully capture FRP variation. With knowledge about the presented stimulus – and the participants' exact gaze positions on it – this should be possible in principle.

Fixation matching. Unfortunately, in much of the existing literature on FRPs (and SRPs), important covariates like saccade size were not recorded (due to the lack of ET) or the problems of correlated response overlap and signal variation were ignored, leaving the results difficult to interpret. One notable exception is a study by Burdette et al. (1986) who concluded that "subtle cognitive influences on this waveform may be studied only under the most rigorous experimental conditions where stimulus and motor parameters are carefully controlled" (p. 531). To address this problem, these authors compared SRPs during reading to those in a "non-cognitive" control condition, in which the participant's gaze tracked a light source that jumped over the screen and "replayed" the individual's eye movement pattern during reading.

The offline equivalent of this approach is *post-hoc fixation matching* (see Publication 3; Luo et al., 2009; for a formalized matching procedure see Kamienkowski et al., 2012). Here, two experimental conditions are made orthogonal by selecting subsets of fixations which are maximally similar with regard to one or more covariates (such as the amplitude of the preceding saccade) and by discarding the rest. Theoretically, a perfect matching of saccade parameters (amplitude and direction) also supersedes the need for ocular artifact correction, since the artifact is held constant. While simple and transparent, such a matching *ex post facto* has its drawbacks. The fixation sample is not only diminished, but systematically biased (Blalock, 1967), and unless conditions are similar in the first place (i.e. only weakly correlated to the covariate), it is only possible to equate a small number of confounding variables.

Statistical control. A more promising perspective for future FRP research is statistical control. A major challenge will be the development of a full model of the waveform at the level of individual fixations. Over the last years, various authors have used linear regression techniques to disentangle the influences of continuous predictors on EEG responses at the single trial level (e.g., Amsel, 2011; Dambacher et al., 2006; Dandekar et al., 2012; Hauk et al., 2006; Pernet, Chauveau, Gaspar, & Rousselet, 2011; Rousselet et al., 2009). In Publication 3, we employed linear mixed models (see also Amsel, 2011) to control for the influences of linguistic covariates and saccade amplitude on FRP amplitude in one time bin. In these models, we did not attempt to compensate for the influence of overlapping potentials, because any change in fixation duration is expected to have a highly non-linear effect on the FRP measured at a given electrode and time point (because complex waveforms are convolved with each other). Nonetheless, future models could estimate the entire waveform (Dandekar et al., 2012) and also incorporate non-linear terms. Ultimately, the goal will be to accomplish the treatment of artifacts, the deconvolution of overlapping responses, the control of visuomotor covariates, and the study of cognitive influences all within a single model of the FRP.

Conclusion

The simultaneous recording of eye movements is a useful addition to established EEG methodology. It improves the understanding of datasets recorded during steady fixation, helps to integrate findings from EEG and eye-tracking studies, and extends the EEG's methodological scope to the study of natural vision.

Original publications

1. Human microsaccade-related visual brain responses[10]

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Abstract

Microsaccades are very small, involuntary flicks in eye position that occur on average once or twice per second during attempted visual fixation. Microsaccades give rise to EMG eye muscle spikes that can distort the spectrum of the scalp EEG and mimic increases in gamma band power. Here we demonstrate that microsaccades are also accompanied by genuine and sizeable cortical activity, manifested in the EEG. In three experiments, high-resolution eye movements were co-recorded with the EEG; during sustained fixation of checkerboard and face stimuli, and in a standard visual oddball task that required the counting of target stimuli. Results show that microsaccades as small as 0.15° generate a field potential over occipital cortex and midcentral scalp sites 100-140 ms after movement onset, which resembles the visual lambda response evoked by larger voluntary saccades. This challenges the standard assumption of human brain imaging studies that saccade-related brain activity is precluded by fixation, even when fully complied with. Instead, additional cortical potentials from microsaccades were present in 86% of the oddball task trials and of similar amplitude as the visual response to stimulus onset. Furthermore, microsaccade probability varied systematically according to the proportion of target stimuli in the oddball task, causing modulations of late stimulus-locked ERP components. Microsaccades present an unrecognized source of visual brain signal that is of interest for vision research and may have influenced the data of many ERP and neuroimaging studies.

[10] published in 2009 in the *Journal of Neuroscience, 29,* 12321-12331

Introduction

When the eyes fixate a stationary object, they are never completely motionless, but perform tiny, seemingly erratic fixational eye movements (FEM). The most prominent contribution to FEM is generated by microsaccades, small (a few arc-min to 1.0°), high-velocity flicks in eye position that are embedded into slower drifting movements at an average rate of 1-2 per second (Martinez-Conde et al., 2004).

Despite early reports that FEM are necessary to counteract neuronal adaptation and perceptual fading (Ditchburn & Ginsborg, 1952), a functional relevance of microsaccades for normal vision has been disputed; and some authors suggested that microsaccades reflect oculomotor noise with no useful purpose (Kowler and Steinman, 1980). However, there is now mounting evidence that microsaccades are intimately related to neuronal processing throughout the visual and attentional system. In humans, the occurrence of microsaccades has been linked to the visibility of parafoveal and peripheral stimuli (Martinez-Conde et al., 2006) and perceptual alternations during multistable vision (van Dam and van Ee, 2006; Laubrock et al., 2008; Troncoso et al., 2008a; 2008b). Microsaccades are not only correlated with visual awareness, but also with visuospatial attention (e.g. Hafed and Clark, 2002; Kohama and Usui, 2002; Engbert and Kliegl, 2003; Laubrock et al., 2005), and their rate is influenced by higher-level cognitive processes, such as the task relevance and relative frequency of visual or auditory stimuli (Valsecchi et al., 2007; 2009; Valsecchi and Turatto, 2007; 2009).

In monkey, intracranial recordings have shown that microsaccades modulate neuronal firing in thalamic (Martinez-Conde et al., 2002; Reppas et al., 2002), striate (Leopold and Logothetis, 1998; Martinez-Conde et al., 2000; 2002), and extrastriate (e.g. Bair and O'Keefe, 1998; Herrington et al., 2009) areas of the visual system. In monkey V1, microsaccades correlate with bursts of spikes (Martinez-Conde et al., 2000) and account for much of the neuronal response variability during visual stimulation (Gur et al., 1997).

These findings raise the question whether microsaccades also generate measurable cortical activity in humans. The potential relevance of microsaccades to EEG research was recently demonstrated by Yuval-Greenberg et al. (2008): Like saccades, microsaccades are accompanied by extraocular muscle activity, which propagates to the EEG as a saccadic spike potential (SP, Thickbroom & Mastaglia, 1986). When data is analyzed in the frequency domain, SPs translate to broadband artifacts in the EEG spectrum. Because experimental

conditions may differ in the relative number of microsaccades, this can mimic changes in induced gamma band power.

However, muscle spikes may not be the only non-invasively recordable electrophysiological concomitant of microsaccades. Although largely unnoticed by the scientific community on FEM, three early EEG studies (Gaarder et al., 1964; Armington et al., 1967; 1974) recorded from a single occipital channel and reported a contrast-sensitive potential after "fine eye movements", which qualify as microsaccades according to current understanding. Despite these early findings and the ubiquity of microsaccades during any fixation task, FEM have not been considered as a relevant source of cortical activity in human cognitive neuroscience. The goal of the present study was therefore to investigate human microsaccade-related brain activity and its potential impact on EEG measurements. High-resolution FEM were co-recorded with the EEG during sustained fixation of typical experimental stimuli (Exp. 1 and 2) and in a classic event-related EEG paradigm (Exp. 3).

Materials and Methods

Experiment 1: Checkerboard fixation

Subjects

Eight healthy adults (5 women, age 21-37, right-handed) participated after providing written informed consent. Subjects had normal uncorrected visual acuity (Bach, 1996) and were naïve as to the purpose of the experiment.

Experimental protocol

Subjects were seated in an electrically shielded, sound-attenuated and dimly lit cabin at a distance of 60 cm from a 22" CRT monitor (Iiyama Vision Master Pro 510, resolution 1024 × 760 pixel, vertical refresh 70 Hz). They were presented with a stationary, black-and-white checkerboard (37° × 28°, 1 cycle per degree, 34 cd/m^2 mean luminance, 94% contrast) that contained five 0.2° fixation points on its horizontal meridian (see Figure 1.1a).

In block 1, the subjects' only task was to maintain perfect fixation on the central red fixation point during 31 trials. Each fixation trial lasted 10 s, but was immediately aborted and repeated if the subject blinked or if a gaze sample deviated more than 2° from the fixation point. This occurred in 35% of the trials. In blocks 2 and 3, subjects performed self-paced horizontal saccades (here: "macrosaccades") between pairs of blue (1.5° apart) and yellow (4.5° apart) points that were located symmetrically to the left and right of the central

fixation point. Because points were separated by odd numbers of checkers (3 or 9), a precise saccade resulted in a transsaccadic inversion of the retinal image (e.g. Riemslag et al., 1987). Subjects were instructed to execute saccades at an approximate pace of 0.6 Hz. Pacing was indicated by five beep tones played before the start of each 90 s saccade trial.

Eye-movement recording

Fixational eye movements were recorded monocularly from the right eye with an infrared video-based eye tracker (IView-X Hi-Speed 1250, SMI GmbH, Germany) at a sampling rate of 500 Hz and an instrument spatial resolution of 0.01°. Viewing was binocular. Head position was stabilized via the inbuilt chin and forehead rests of the eye tracking column. After every fifth trial, the system was recalibrated with a 13-point grid.

EEG recording

The EEG was recorded from 60 Ag/AgCl scalp electrodes (including low electrode sites, e.g. FT9, PO9, Iz) mounted in a cap at standard 10-10 positions (American Electroencephalographic Society, 1994). Additionally, electro-oculogram (EOG) electrodes were affixed at the outer canthus and infraorbital ridge of each eye. Frontal electrodes were foam-cushioned to avoid pressure artifacts from the forehead rest. An electrode on the vertebra prominens served as ground. EEG and EOG channels were referenced against left mastoid (M1) during recording and re-referenced offline against the average of all electrodes. Impedances were kept below 5 kΩ. The EEG was amplified with a Brainamp DC amplifier (Brain Products GmbH, Germany), digitized at 500 Hz with a bandpass from DC to 100 Hz, and high-pass filtered offline at 1 Hz (12 dB/octave). For dipole modeling, 3D electrode locations were acquired with a CMS20 digitizer (Zebris Medical GmbH, Germany). EEG and FEM recordings were synchronized via a common TTL pulse, sent from the presentation PC (running Presentation Software, Neurobehavioral Systems Inc., USA) to both systems before and after each trial.

Microsaccade detection

Microsaccades were detected in 8 s intervals beginning 1 s after checkerboard onset and ending 1 s before offset. Microsaccades were defined as outliers in 2D velocity space using the algorithms detailed in Engbert and Mergenthaler (2006, MATLAB functions downloadable at www.agnld.uni-potsdam.de/~ralf): First, eye velocity was computed with a modified version (Engbert and Mergenthaler, 2006) of a central difference algorithm (Bahill et al., 1982) to suppress high-frequency noise. Microsaccades were then defined as

parts of the eye movement trajectory where velocity (combined for the vertical and horizontal movement component) exceeded a relative velocity threshold for a minimum duration of 3 samples (6 ms). The velocity threshold was set to 5 median-based SDs of the velocity values observed in the entire 8 s interval. Additionally, microsaccades were required to have a magnitude < 1° and a temporal distance from the previous microsaccade of > 50 ms. Saccade magnitude was defined as the Euclidean distance between the start and end point of the movement. Identical parameters were used to detect macrosaccades, but minimum magnitude was set to 1° to exclude microsaccades and corrective saccades in these blocks.

Microsaccade-locked EEG

An EEG segment of 1024 ms (-400 to 624 ms) was cut around the onset of each detected microsaccade and baseline-corrected by subtracting from each channel the mean voltage in the 100 ms interval before microsaccade onset. Segments with absolute voltages > 150 μV in any channel (2% of segments) were discarded to exclude non-ocular artifacts from voltage drifts or amplifier saturation. To obtain microsaccade-locked ERPs, segments were averaged first within and then across subjects. The same averaging procedure was applied to voluntary saccades in block 2 and 3.

For fixation trials, additional averages were computed for microsaccades of different magnitude (using five magnitude bins: < 0.2°, 0.2-0.25°, 0.25-0.35°, 0.35-0.45°, > 0.45°). To generalize analyses to all types of FEM (including slower drift intervals), the EEG was also averaged as a function of instantaneous eye velocity at each eye tracker sampling point, irrespective of whether a sample belonged to a detected microsaccade or not. For each eye sample, the 150 ms of EEG data following the sample were assigned to one of 25 eye velocity bins (between 0 and 80°/s; upper bin limits were defined by 1.2^n °/s, with n = 1…24) and subsequently averaged.

Corneoretinal artifact

Rotation of the bulbus' electrostatic potential (Berg and Scherg, 1991) distorts the signal at electrodes around the eyes. To quantify this corneoretinal artifact (cf. Figure 1.2c), micro- and macrosaccades were classified as either left- or rightwards-oriented according to their horizontal movement component. Artifact amplitude was then defined as the mean voltage difference between the horizontal EOG electrode ipsilateral and contralateral to saccade direction in the interval 50-100 ms after saccade onset.

Dipole modeling

Generators of microsaccade-related brain potentials were modeled with equivalent current dipoles in BESA (Brain Electromagnetic Source Analysis, v5.1, Megis GmbH, Germany) using a four-shell spherical head model. Both one- and two-dipole models have been used to model the lambda response following macrosaccades (Kazai and Yagi, 2003) and the P1 visual evoked potential (VEP, Tobimatsu and Celesia, 2006); here we used a pair of dipoles with the constraint of a bihemispheric mirror-symmetric location (e.g. Di Russo et al., 2005). First, two regional sources (each consisting of three orthogonal dipoles) were fitted to the maximum in global field power (GFP; the SD across electrodes) between 75 and 125 ms after microsaccade onset. Each regional source was then oriented and its predominant dipole was retained. The model was fitted both to the grand average microsaccade-locked ERP and to each subject average.

Frequency domain

To test the influence of microsaccade-related muscle and brain potentials on the EEG spectrum, microsaccade-locked segments were subjected to a wavelet-based time-frequency analysis (see *Supplementary Materials*).

Experiment 2: Face fixation

Subjects and experimental protocol.

Three subjects (2 women, age 26-31, uncorrected normal acuity), naïve and different from those in Exp. 1, were instructed to maintain perfect fixation on a 0.2° point presented in the center of a stationary image of a face (Figure 1.3a). Images were derived from a stimulus set previously used in ERP studies on face processing (e.g. Schacht et al., 2008). Each image showed a 7.5° × 8.5° frontal view of a face with frontal gaze direction and without external features (e.g. hair), presented on a homogeneous 14 cd/m^2 gray background. Six different images were repeatedly shown in 48 fixation trials per subject, each lasting 10 s. Recording hardware, fixation procedure, microsaccade detection, and EEG analyses were identical to Exp. 1.

Experiment 3: Visual oddball task

To assess the presence of microsaccade-related brain potentials in typical event-related EEG data, we reanalyzed data from a visual oddball experiment with simultaneous FEM recording (Valsecchi et al., 2009).

Subjects

Subjects were twelve healthy adults (9 female, age 20-29) with self-reported normal acuity and normal color vision (Ishihara, 2003). The sample included two authors (OD, MV); the other subjects were naïve as to the purpose of the experiment.

Experimental protocol

Subjects were instructed to minimize eye blinks and to maintain fixation on a 0.48° white point that was continuously displayed on an otherwise empty black screen. Once per second, a red or green disc with a diameter of 2.04° appeared for 100 ms around the fixation point (see Figure 1.4a). The subject's task was to count silently the stimuli with the pre-specified target color. Every 50 trials, presentations were paused and subjects entered the number of targets with a keyboard. Stimuli were presented on a 19" CRT monitor (LG Flatron 915FT, 1024 × 768 pixel, vertical refresh 100 Hz) at a viewing distance of 75 cm. Luminance of red and green discs was matched using 25 Hz flicker fusion (Ives, 1912) and the assignment of target color (red or green) was counterbalanced over subjects.

In three experimental blocks (500 trials each), the frequency of target stimuli was 20, 50, or 80%. Both target status (target or non-target) and stimulus frequency are known to modulate the amplitude of the P300 component of the ERP in oddball tasks (Duncan-Johnson and Donchin, 1977).

Eye-movement recording

FEM were recorded from the right eye with an IView-X Hi-Speed eye tracker (SMI GmbH, Germany; 238 Hz model) at a sampling rate of 238 Hz and an instrument spatial resolution < 0.025°. Viewing was binocular. The system was calibrated every 50 trials with a 9-point grid. Calibration quality was assessed every 10 trials and additional recalibrations were performed if necessary.

EEG recording

Data was recorded from 36 Ag/AgCl electrodes located at standard 10-10 positions and four periocular EOG electrodes at a sampling rate of 250 Hz and a bandpass from 0.1 to 70 Hz. All channels were referenced against left mastoid and converted to average reference offline.

Data analysis

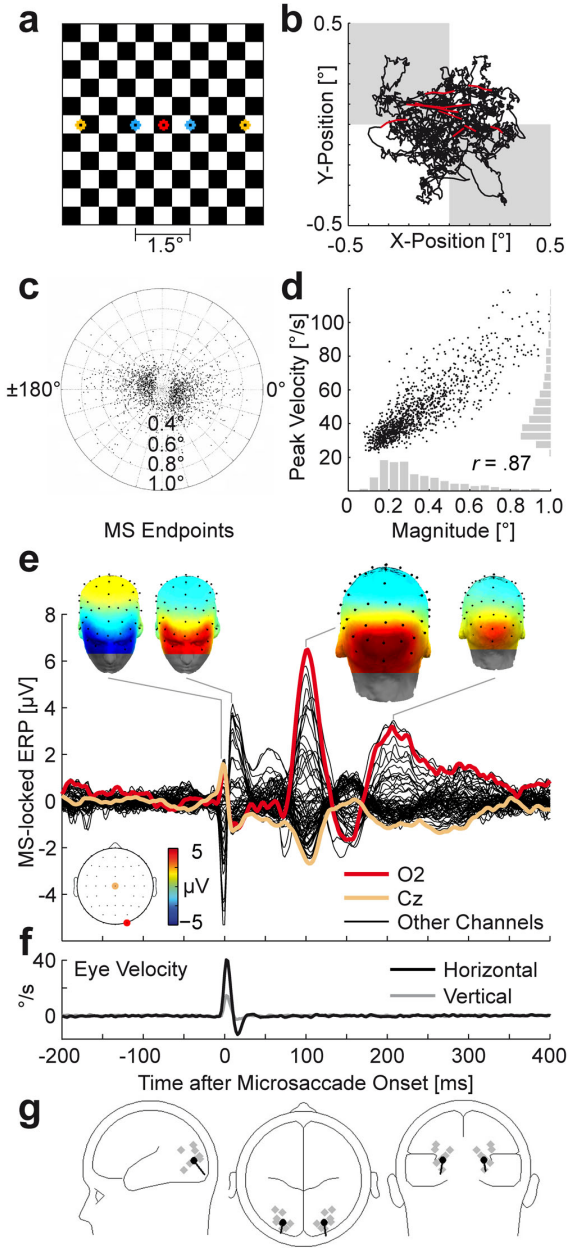
Eighty-six percent (n = 15,732) of all trials were free of eye blinks and used in subsequent analyses. In each trial, lasting from -100 to 1000 ms after stimulus onset, microsaccades were detected with the same algorithm (Engbert and Mergenthaler, 2006), but detection parameters were adjusted to the lower sampling rate of the eye tracker (min. duration: 4 samples; velocity threshold: 6 SD). Two sets of EEG segments were extracted: The first was time-locked to microsaccade onsets and averaged to visualize microsaccade-related potentials (cf. Figure 1.4b). The second was cut around stimulus onsets.

Two analyses were performed on the stimulus-locked segments: In analysis 1, segments were sorted according to the latency of the first microsaccade in the trial (Figure 1.4c-e) using the *erpimage* function of the EEGLAB toolbox (Delorme and Makeig, 2004) for MATLAB (The Mathworks Inc, Natick, MA). For visualization, microsaccade-sorted trials were smoothed with a moving average across 20 (Figure 1.4c) or 70 (Figure 1.4d-e) adjacent segments after sorting. In analysis 2, the ERP from all trials (overall ERP) was compared to the ERP from two subsets of trials: trials with (MS-present ERP) and trials without (MS-absent ERP) a microsaccade. Because few trials (14%) were completely free of microsaccades, the absent-present split was not based on the complete trial, but on microsaccade occurrence between 200-400 ms. This interval corresponds to the typical latency of the post-stimulus rebound in microsaccade probability during which most experimental effects on microsaccade behavior have been observed in previous studies (e.g. Engbert and Kliegl, 2003; Valsecchi et al., 2007).

MS-present and MS-absent trials were averaged separately for each subject and condition (targets/non-targets with 20%, 50%, 80% frequency). To test whether microsaccades influence stimulus-locked ERPs, MS-present ERPs and MS-absent ERPs were compared at four electrodes on the posterior sagittal midline: Cz, Pz, Oz, and Iz. Mean ERP voltages between 350-550 ms after stimulus onset were submitted to repeated-measures ANOVAs on factors *electrode*, *stimulus frequency*, and microsaccade *presence* (MS-present vs. MS-absent). Separate ANOVAs were conducted for target and non-target trials. To correct for violations of the sphericity assumption, p-values were corrected according to Huynh-Feldt. If microsaccadic brain potentials influence ERPs, this influence should be larger in conditions with more and smaller in conditions with fewer microsaccades. Analogous tests were therefore performed on the difference between the overall ERP and the MS-absent ERP. Whereas the absent-present split compares two extreme scenarios (microsaccade in *none* of the trials vs. microsaccade in *every* trial), irrespective of actual microsaccade rate,

the comparison between overall and MS-absent ERPs takes into consideration the varying proportion of microsaccade trials in different experimental conditions. As a global measure of ERP distortion, we computed for each condition the GFP of the difference between grand-mean overall ERP and grand-mean MS-absent ERP.

Figure 1.1



Microsaccade-related potentials during checkerboard fixation. **a,** Central part of the checkerboard with fixation point (red) and voluntary saccade targets (blue and yellow). **b,** Typical trajectory of the right eye during 10 s of attempted fixation. Data points belonging to microsaccades are plotted in red. Background shading symbolizes the checkerboard's check size. **c,** Spatial distribution of 1,225 microsaccades. The center represents the microsaccade starting point, dots indicate endpoints. **d,** Microsaccades showed the typical correlation between peak velocity and magnitude. Marginal distributions are plotted in gray. **e,** Grand average ERP, time-locked to microsaccade onsets (Time 0). Signals at all EEG and EOG channels are plotted superimposed; electrodes over right occipital cortex (O2) and the vertex (Cz) are highlighted. Inserts show scalp distributions at selected time points. Microsaccade onset was accompanied by a biphasic muscle spike potential (SP) with periocular maxima. After 106 ms, microsaccades evoked a microsaccadic lambda response (MLR) with maxima over visual cortex and, with reversed polarity, vertex. **f,** Grand mean eye velocity from simultaneous eye tracking. Negative velocities represent movements against the predominant direction of the microsaccade. **g,** Two-source equivalent dipole model, fitted to the MLR peak. Dipole estimates for single subjects are plotted in gray.

Results

Checkerboard fixation

Figure 1.1b shows a typical eye movement trajectory during 10 s of checkerboard fixation. On average, 153 microsaccades were detected per subject in 247 s of analyzed fixation. This relatively low microsaccade rate (0.62 Hz) is consistent with findings that subjects can voluntarily suppress some of their microsaccades if strong fixation instructions are given during prolonged fixation (Steinman et al., 1967). The median of microsaccade magnitude was 0.29° (SD of median across subjects: ±0.06°), median peak velocity was 48.1°/s (±12.4), and median duration was 10.0 ms (±1.5). Eighty-five percent of microsaccades were smaller than 0.5°. In agreement with previous research, most microsaccades were oriented horizontally (see Figure 1.1c). Microsaccade peak velocity and magnitude were highly correlated (r = .87) and followed the "main sequence'" (Zuber et al., 1965) characteristic for saccadic movements (Figure 1.1d and supplementary Figure S1.1).

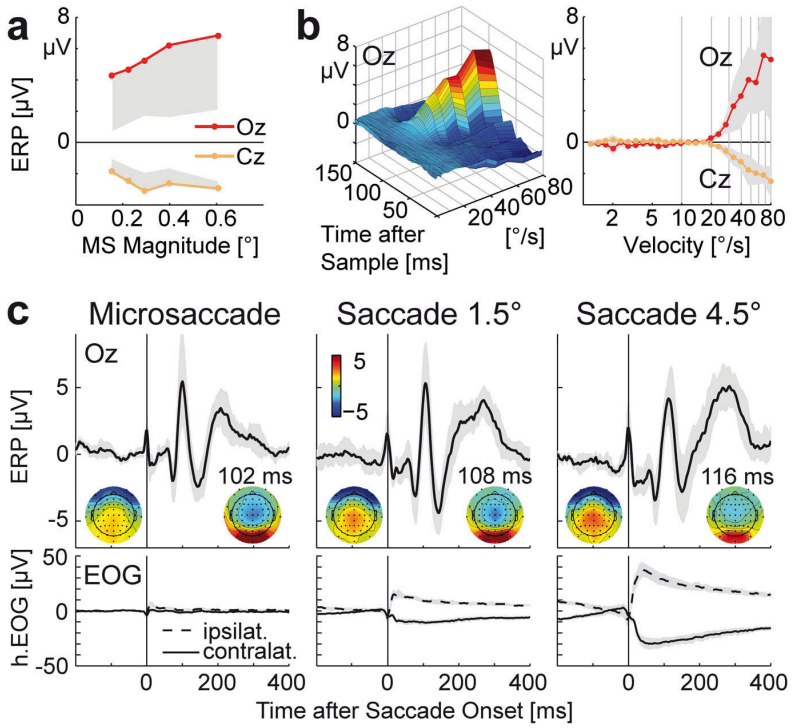
Microsaccadic lambda response

Figure 1.1e shows the grand averaged ERP, time-locked to microsaccade onset. A key finding of the present study is that microsaccades evoked a large potential peaking M = 106 ms (SD ±3.5, at electrode O2) after movement onset. We will refer to this potential as *microsaccadic lambda response* (MLR) because – as we will argue – it closely resembles the lambda response observed after macrosaccades (Thickbroom et al., 1991; Kazai & Yagi, 2003). Maxima of the MLRs were observed over right visual cortex (electrode O2) and – with opposite polarity – at mid-central electrode Cz with a peak voltage difference between both electrodes of M = 9.6 μV (±5.6, range across subjects: 4.2-18.9 μV). The dominant MLR was followed by a second occipital peak at 208 ms, which has been observed in similar form after voluntary 1° saccades on checkerboard stimuli (Riemslag et al., 1987).

Dipole modeling produced MLR source locations in occipital cortex (Figure 1.1g). Talairach dipole coordinates for the grand average-based, two-dipole model were x = ±24 mm (±6), y = -82 mm (±11), and z = 3 mm (±9, SDs are based on the variance between single subject models), corresponding to locations in the middle occipital or lingual gyri. Residual model variance was < 2% at the MLR peak. However, because of the limited spatial resolution of EEG inverse models, the data allowed no distinction whether striate or early extrastriate sources accounted for the MLR.

Figure 1.2a shows MLR peak amplitude as a function of microsaccade magnitude. At occipital electrodes, amplitude increased monotonically from smaller to larger microsaccades (Figure 1.2a). Using 95% between-subject confidence intervals (CIs) as a criterion, significant MLRs were observed even for the smallest bin of microsaccades with a median magnitude of 0.15°. Figure 1.2b (left panel) shows occipital EEG voltage as a function of instantaneous eye velocity at every sample during the fixation interval. Faster movements were followed by an occipito-central potential after 100 ms (the latency shown in Fig 2b, right panel) and this effect was significant for velocities > 22 °/s. Occipital potentials were therefore restricted to movements in the velocity range of microsaccades, but not measurable at slower eye velocities. In the frequency domain, the transient MLR waveform translated to increased spectral power in the theta and lower alpha band at occipital electrodes about 100 ms after microsaccade onset (see Figure S1.2).

Figure 1.2



Lambda response as a function of microsaccade magnitude, eye velocity, and saccade type. **a,** MLR amplitude after 100 ms as a function of microsaccade magnitude. Shading gives the 95% between-subject CI in one direction. **b,** *Left:* EEG voltage at occipital electrode Oz as a function of instantaneous eye velocity during fixation. *Right:* Voltage 100 ms after the velocity sample. Significant responses are seen after velocities > 22 °/s. **c,** Comparison of potentials evoked by microsaccades and larger voluntary saccades. *Top*: Electrode Oz. Inserts show scalp topographies at movement onset (0 ms) and at the peak latency of the lambda response. Note

the similarity between the micro- and macrosaccadic lambda response despite large differences in saccade magnitude. *Bottom*: Corneoretinal artifacts are evident as a voltage difference between the horizontal EOG electrodes ipsilateral and contralateral to saccade direction. Note the small artifact for microsaccades.

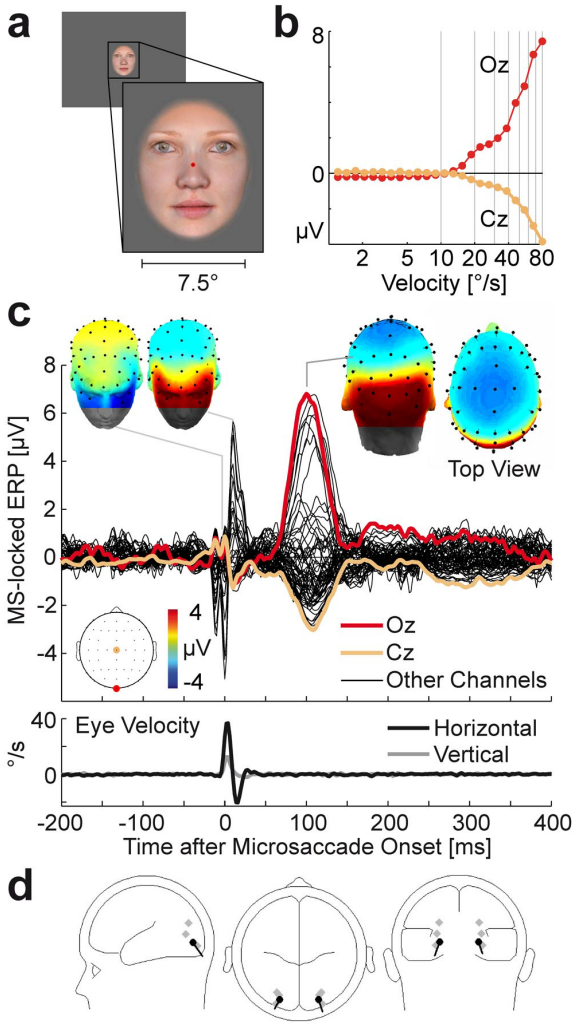
Comparison to voluntary saccades

Microsaccadic potentials were compared to those evoked by macrosaccades of 1.5° (median magnitude, peak velocity, and duration: 1.61°, 159.7°/s, and 15.1 ms, respectively) and 4.5° (4.71°, 283.3°/s, and 30.1 ms, respectively). Figure 1.2c (top) shows that despite large differences in magnitude, micro- and macrosaccades evoked lambda responses with very similar scalp distributions and comparable peak amplitudes. All saccade types were accompanied by a corneoretinal artifact (Figure 1.2c, bottom). Artifact size was proportional to saccade magnitude with a mean effect in the bipolar EOG of 2.3, 21.5, and 61.5 μV for microsaccades, 1.5°, and 4.5° saccades, respectively. The microsaccadic corneoretinal artifact was therefore not only considerably smaller than the microsaccadic brain potential, but far too small to exceed the EOG-based rejection thresholds (typically set to 20-100 μV) commonly applied to identify EEG segments with blinks or saccades.

Spike potential

Our data replicates recent reports of a microsaccadic spike potential in the EEG (Yuval-Greenberg et al., 2008; Reva and Aftanas, 2004; Trujillo et al., 2005). While cerebral contributions to the SP have been discussed (Nativ et al., 1990; Parks and Corballis, 2008), it is generally thought to originate in the extraocular muscles and to reflect a summation of EMG spikes during the maximal recruitment of motor units at saccade onset (Moster and Goldberg, 1990; Sparks, 2002). Microsaccades, in particular, are accompanied by an EMG burst in the agonistic rectus muscle that begins 5 ms before movement onset (Yamazaki, 1968). The SP peaked at microsaccade onset (0 ms, ±1.0 ms) and was largest as a negative deflection at the infra-orbital EOG electrode ipsilateral to microsaccade direction (Thickbroom and Mastaglia, 1986) and as a positive deflection at the vertex (Figure 1.1e). In the frequency domain, the transient SP translated to a broad band artifact in the high beta and gamma band around microsaccade onset (see Figure S1.2).

Figure 1.3



Microsaccade-related potentials during face fixation. **a,** Example stimulus. **b,** EEG voltage as a function of instantaneous eye velocity 100 ms earlier. **c,** Grand average microsaccade-locked ERP. The double spike at microsaccade onset is due to an individual subject for whom the SP preceded movement onset by 10 ms. This caused a doubled SP in the grand average ERP (see also Supplementary Figure S1.3). **d,** Dipole model at the peak of the MLR.

Face fixation

Experiment 2 tested whether the large microsaccadic lambda response was specific to the full-screen, high-contrast checkerboard or whether it generalizes to the fixation of smaller face stimuli (Figure 1.3a). This material is typical of the pictorial stimuli often used in cognitive neuroscience.

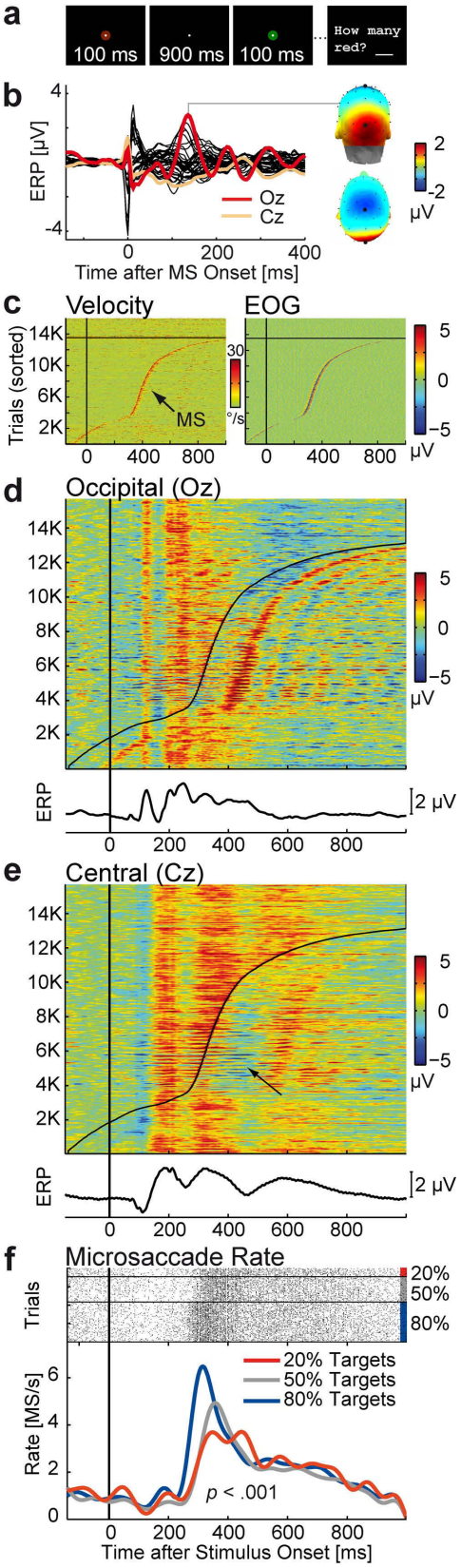
While fixating the faces, subjects made an average of 337 microsaccades in 382 s of fixation, corresponding to an average rate of 0.88 Hz. Movement kinematics were similar to Exp. 1,

with a median magnitude of 0.27° (±0.07), peak velocity of 43.9°/s (±13.1), and duration of 10.0 (±0.0) ms (Figure S1.1). Figures 1.3b and 1.3c show the microsaccade-locked EEG and its relationship to eye velocity: Again, microsaccades evoked an MLR that peaked after M = 104 ms (±8.0) with a mean Oz-Cz voltage difference of 10.6 μV (±1.2). Dipoles for the two-dipole model were localized in the middle occipital gyri (x = ±23 mm (±2), y = -85 mm (±8), and z = 6 mm (±7), see Figure 1.3d) with a residual variance < 1%. Thus, the MLR resembled that from Exp. 1 in terms of latency, amplitude, scalp topography, and estimated dipole source.

Visual oddball task

Results of experiments 1 and 2 imply that MLRs may be frequently present during EEG recordings that require steady fixation. Experiment 3 therefore tested the presence and impact of MLRs in a classic paradigm for eliciting cognitive ERP components, the visual oddball task.

Figure 1.4



Microsaccade-related potentials in the oddball experiment. **a**, Trial scheme: Subjects silently counted discs of the target color. **b**, Grand average ERP, time-locked to the onset of microsaccades detected during experimental trials. The MLR peaked after 136 ms over visual cortex and the vertex. **c**, Eye velocity and EOG voltage (color-coded) in 15,732 experimental trials. Each horizontal line represents the data of one trial; Time 0 marks stimulus onset. Trials are sorted from bottom to top according to the latency of the first microsaccade detected in the trial. Trials with no microsaccade are plotted above the black line. Left: Rectified velocity of the right eye. Microsaccades are evident as a peak in eye velocity. Right: Signal at the right infraorbital EOG electrode, high-pass filtered at 30 Hz. The SP is visible as a spike at microsaccade onset. **d**, Sorted trials at electrode Oz. Microsaccade latency is indicated by the black line. The presence of MLRs in the stimulus-locked data becomes apparent after sorting. **e**, MLRs have a negative polarity at Cz. The positive-going P300 component is therefore attenuated in trials in which a microsaccade occurred 200-300 ms after stimulus onset (arrow). **f**, Microsaccade rate for target stimuli. Top: Each horizontal line represents one trial; microsaccades are marked with dots. Bottom: Microsaccade rate, smoothed with a 10 Hz low-pass filter for visualization. The microsaccadic rebound was significantly smaller in blocks with rare (20%) compared to blocks with frequent (80%) target stimuli.

MLRs in oddball task

Concurrent eye tracking revealed that on average, subjects made 1,925 microsaccades during 1,311 analyzed trials of the oddball experiment (or 1.47 per second). Microsaccades had a median magnitude of 0.23° (±0.07, Figure S1.1) and were again accompanied by both SP and MLR (see Figure 1.4b); the latter peaked at Oz after 136 ms, but also had a negative maximum at Cz with a Oz-Cz difference of M = 3.97 μV (±2.1, range 1.7-9.1 μV). The MLR was therefore considerably smaller and more delayed relative to Exp. 1 and 2. This difference is probably explained by differences in retinal stimulation: 95% of the microsaccades occurred during the inter-stimulus interval when the only stimulus was the 0.48° fixation point. Still, MLR amplitude was as large as that of the P1 visual component elicited by the trial-initial onset of the disc stimulus (Figure S1.4). In several subjects, the initial MLR peak was followed by a damped oscillation at occipital sites (cf. Figures 1.4b and 1.4d), which resembled the post-stimulus alpha ringing sometimes observed in VEPs (e.g. Makeig et al., 2002).

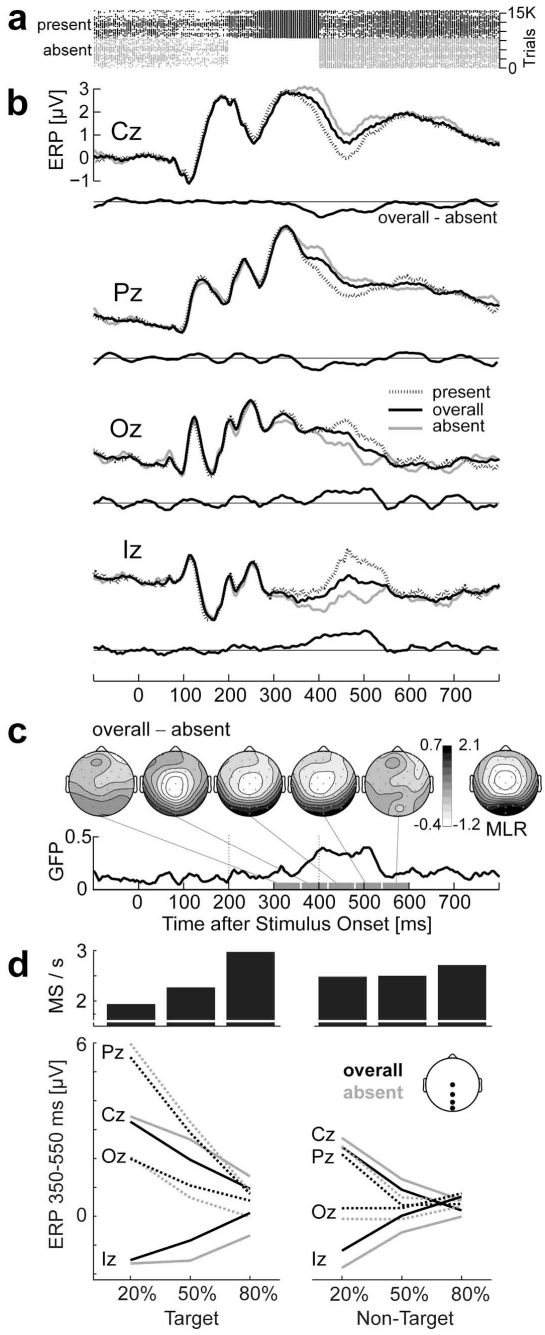
Of all experimental trials, 86% contained at least one microsaccade. The presence of microsaccadic muscle and brain potentials became evident when stimulus-locked EEG segments were sorted according to the latency of the first microsaccade in each trial: While the SP is seen best in the high-pass filtered data from infraorbital EOG electrodes (Figure 1.4c, right panel), the strong overlap with MLRs is evident even in the unfiltered EEG, both at occipital electrodes (Figure 1.4d) and, with reversed polarity, at mid-central electrodes (Figure 1.4e). This means that early visual processing areas were engaged at least twice in a typical trial (Figure 1.4d).

Microsaccade rate effects

Figure 1.4f shows the rate of microsaccades after the presentation of target stimuli. Microsaccade rate has been shown to follow a stereotypical time course after sensory events, with an early inhibition followed by a later rebound (Engbert & Kliegl, 2003; Rolfs et al., 2008). This was also observed here: Microsaccade probability decreased temporarily after stimulus onset, but then increased strongly after about 200 ms and reached a maximum at 320 ms. Importantly, magnitude and latency of the rebound differed as a function of the frequency of target stimuli in the experimental block: Microsaccade rate was significantly lower after the presentation of rare (20%) compared to frequent (80%) target stimuli (ANOVA on the effect of target stimulus frequency on microsaccade rate between 220 and 420 ms, $F(2,22) = 21.2$; $p < 0.001$, for details see Valsecchi et al., 2009). Additionally, the peak latency of the rebound was delayed for rare stimuli; $F(2,22) = 12.1$,

$p < 0.001$. No effects of stimulus frequency were observed for non-targets. These results corroborate previous findings that the microsaccadic rebound is decreased in response to infrequent task-relevant stimuli in visual (Valsecchi et al., 2007; Valsecchi and Turatto, 2007) and auditory (Valsecchi and Turatto, 2009) oddball tasks.

Figure 1.5



Stimulus-locked ERP in the oddball experiment as a function of microsaccade occurrence between 200-400 ms. **a,** Horizontal lines represent trials; dots mark microsaccades (MS). MS-present and MS-absent trials are plotted separately. **b,** ERP for MS-absent trials, MS-present trials, and the overall set of trials. Central electrodes show negative and occipital electrodes positive deflections in trials with microsaccades. Difference waves compare the ERP from all trials to that from MS-absent trials only. Note that experimental conditions are equally weighted in this plot, i.e., MS-absent, MS-present, and overall ERPs were first computed in each condition, and only then collapsed across conditions. **c,** Scalp topography and global field power of the microsaccade effect. Its topography (shown for 60 ms intervals between 300-600 ms) resembled the peak topography of the MLR (shown for comparison) and its latency reflected the delay between microsaccade onset and MLR peak. **d,** Mean microsaccade rate (between 200-400 ms) and ERP amplitude (350-550 ms) for the six conditions. In addition to P300 effects of targetness and stimulus frequency, ERP distortions from microsaccades are evident at all electrodes. For non-targets, both microsaccade rate and ERP distortions were similar for rare and frequent stimuli. For targets, distortions increased with increasing microsaccade rate at occipital electrodes.

ERP modulation from MLRs

o assess the impact of MLRs on stimulus-locked ERPs, we compared the ERP from trials with (56%) and without (44%) a microsaccade during the rebound interval (Figure 1.5a). Figure 1.5b shows that ERP waveforms were systematically modulated as a function of microsaccade occurrence: In trials with microsaccades, occipital electrodes showed more positive and central electrodes more negative voltages, respectively. This polarity reversal of the microsaccade effect yielded an *electrode* × *microsaccade presence* interaction on ERP amplitude between 350-550 ms, for both target, $F(3,33) = 28.4$, $p < .001$, $\eta_p^2 = 0.72$, and non-target stimuli, $F(3,33) = 15.4$, $p < .001$, $\eta_p^2 = 0.58$. Post-hoc tests at individual electrodes showed that the difference between MS-absent and MS-present trials was significant ($p < .01$) at all four electrodes for targets and non-targets.

Scalp topography and timing of ERP changes (Figure 1.5c) suggest that they were caused by the additional presence of MLRs: The topography of the effect closely reflected the MLR topography and effects occurred mainly between 350-550 ms, that is, with a delay of about 150 ms relative to the rebound window (200-400 ms). This delay is expected from the MLR peak latency, which was 136 ms in this experiment.

The difference between overall ERP and MS-absent ERP provides a realistic estimate of the additional signal attributable to MLRs. At the midline electrodes tested, the maximum size of this difference (overall minus absent) was -0.68 µV at Cz (at 408 ms), -0.52 µV at Pz (404 ms), +0.63 µV at Oz (504 ms), and +0.85 µV at Iz (508 ms). For the current oddball paradigm, this meant that the large centroparietal positivity of the P300 was decreased by microsaccades in late time segments: Across conditions, ERP amplitude between 350-550 ms was reduced from 2.50 to 2.06 µV at Cz and from 3.37 to 3.05 µV at Pz.

Because microsaccade rate increased with target stimulus frequency, distortions were expected to be smaller in the 20% condition (with 39% MS-present trials) than in the 50% (46% MS-present trials) and 80% condition (59% MS-present trials). GFP of the microsaccade effect (overall minus absent) increased from 0.31 to 0.36 to 0.39 µV for the three frequencies, indicating that distortions increased with microsaccade rate. A condition-specific effect was supported by a three-way interaction electrode × presence (overall vs. absent) × stimulus frequency, $F(6,66) = 3.0$, $p < .05$, $\eta p2 = 0.21$, for target stimuli. Post-hoc tests showed that the *presence* × *stimulus frequency* interaction was strongest at Iz, $F(2,22) = 6.3$, $p < 0.01$, $\eta_p^2 = 0.36$, where the microsaccade effect was 0.12 µV in the 20%, but 0.76 µV in the 80% condition (Figure 1.5d). This interaction was not

significant at Pz, an electrode often used to quantify P300 amplitude. Also, no interaction was observed for non-targets, which also did not differ significantly in microsaccade rate.

In summary, absolute waveforms and topographies of late ERP components were altered by the presence of microsaccadic lambda responses, causing changes in the order of half a microvolt at both central and occipital sites. At occipital sites, distortions tended to increase with increasing microsaccade rate, leading to more positive ERPs for more frequent target stimuli.

Discussion

While the functional relevance of microsaccades has been the subject of intense research, little attention has been given to microsaccade-related activity in the human brain. However, single unit recordings (Martinez-Conde et al., 2004), microsaccade-driven perceptual alternations (e.g. van Dam and van Ee, 2006; Martinez-Conde et al., 2006), and pioneering work from the 60s (Gaarder et al., 1964) indicate that microsaccades could be a relevant source of cortical activity. The current study investigated microsaccade-related potentials and their impact on event-related EEG data. Simultaneous recordings in three groups of subjects, fixating three different stimuli, confirmed that microsaccades are accompanied by a myogenic SP that translates to a spectral artifact in the gamma band (Yuval-Greenberg et al., 2008). Additionally, however, microsaccades generate a sizeable cortical response over the occipital and central scalp, here called *microsaccadic lambda response* (MLR).

A primarily visual origin of the MLR is indicated by its time course, scalp topography, occipital source, and overall resemblance to the lambda response established for macrosaccades. A visual nature of the latter is suggested by its sensitivity to stimulus properties such as contrast and spatial frequency (Gaarder et al., 1964; Kazai and Yagi, 1999), its absence or strong attenuation for featureless or dark visual fields (e.g. Scott & Bickford, 1969; see also Szirtes et al., 1982), its similarity to the VEP to patterns moved at saccade velocities (Riemslag et al., 1987; Thickbroom et al., 1991), and its dipole source, which has been estimated in striate cortex, close to that of the pattern-reversal P1 (Kazai and Yagi, 2003). While there is some evidence for non-visual, corollary signals in the peri- and post-saccadic EEG (Kazai and Yagi, 2003), neither the early latency nor the lateralized topography reported for these potentials (Skrandies and Laschke, 1997) was observed here. It is therefore unlikely that non-visual signals had major contributions to the MLR.

Thus, the MLR most likely reflects a sweep of activation through striate and/or extrastriate cortex following the microsaccade-generated retinal image motion. It may therefore constitute a field-potential analogue of microsaccade-related spike bursts previously observed in monkey V1. Martinez-Conde et al. (2000; 2002) proposed that these bursting responses sum up to large-scale synchronized responses in visual cortex, which would present an effective mechanism to maintain the visibility of stationary stimuli. The fact that MLR amplitude resembled that of macrosaccadic lambda responses and VEPs indicates that extended regions of visual cortex are activated by small retinal displacements. This is consistent with the hypothesis that microsaccades contribute to neural coding in the early visual system (Martinez-Conde et al., 2004) and fits the observation that microsaccades often precede switches in visual awareness during multistable vision (van Dam and van Ee, 2006; Martinez-Conde et al., 2006; Laubrock et al., 2008; Troncoso et al., 2008a; 2008b). Because co-registration allows direct comparisons between MLRs and perceptual states (e.g. visibility), it may help to integrate single cell data with human psychophysics and to investigate the recently established links between microsaccades, visual attention, and cognition.

Methodological implications

The present findings have notable methodological implications. The vast majority of human neuroimaging data (e.g. using EEG, MEG, fMRI) is collected under conditions of sustained fixation. Typical procedures require the subject to fixate steadily during all measurements, based on the assumption that saccade-related brain activity is effectively precluded by fixation.

Results suggest that this assumption is wrong: Even when subjects fixate as precisely as they can, MLRs are frequently overlaid on the EEG. This was apparent in the oddball task, where 86% of the trials contained at least one microsaccade. The presence of MLRs in the stimulus-locked data became immediately evident when trials were sorted by microsaccade latency from concurrent eye tracking. Still, the oddball experiment may have underestimated the typical impact of microsaccades because of the stimulus' small size and short duration. We have recently conducted a follow-up experiment (see Supplementary Materials, Figure S1.5) that required a speeded classification of the faces fixated in Exp. 2. Following common ERP practice, stimuli were presented without an embedded fixation point and remained visible throughout the trial. Under these conditions, 97% of the trials contained small saccades and lambda response amplitude was doubled.

It is therefore possible that many – if not most – event-related EEG datasets contain visual evoked potentials from microsaccades. There are several explanations why these contributions were not considered in previous EEG research: First, microsaccades occur with temporal jitter relative to experimental events. Their contribution is therefore not easily seen in averaged signals. Second, EEG research has traditionally focused on corneoretinal artifacts. These artifacts are (approximately) proportional to saccade magnitude because they result from the rotation of the eye ball's electric dipole (Berg and Scherg, 1991). Microsaccadic artifacts were therefore too small (2.3 μV) to exceed the EOG-based rejection thresholds routinely applied to single-trial EEG data (typically 20-100 μV). The MLR itself, on the other hand, is not detected by artifact rejection methods, as it reflects cortical activity with no topographical resemblance to typical EEG artifacts. Finally, existing EEG (e.g. Kennett et al., 2007), MEG (e.g. Herdman and Ryan, 2007), and fMRI (e.g. O'Connor et al., 2002) studies with eye movement monitoring have typically used eye trackers with insufficient spatiotemporal resolution (e.g. 60 Hz sampling rate) for reliable microsaccade detection.

Condition effects on microsaccades

Microsaccades are not randomly distributed over time. After any sudden onset, their rate drops temporarily below baseline, but rebounds above baseline level between 200-400 ms (Rolfs et al., 2008). This inhibition-rebound sequence is triggered by any visual or auditory stimulus, and even environmental sounds such as the click emitted by TMS stimulation (Kanai et al., 2008).

Importantly, recent studies have demonstrated pervasive effects of experimental factors on the rate, orientation, and magnitude of microsaccades during the inhibition-rebound sequence. These factors include the orientation or location of endogenous (Engbert and Kliegl, 2003; Laubrock et al., 2005) and exogenous (Hafed and Clark, 2002; Rolfs et al., 2004) attentional cues; the locus of sustained visual attention (Kohama and Usui, 2002); the luminance contrast and color contrast of a visual stimulus (Rolfs et al., 2008); stimulus modality (auditory vs. visual, Rolfs et al., 2005; 2008; Valsecchi and Turatto, 2009); the stimulus symbol used in a simple reaction task (Engbert and Kliegl, 2003); a stimulus' task relevance, relative frequency, and sequential order (Valsecchi et al., 2007; 2009; Valsecchi and Turatto, 2007; 2009); the coherence of picture objects (Yuval-Greenberg et al., 2008); and the timing of manual (Betta and Turatto, 2006) and saccadic (Rolfs et al., 2006) responses. In addition, there are large idiosyncratic differences in fixational instability, both

between normal subjects (Nachmias, 1959; Schulz, 1984) and in clinical populations (Martinez-Conde, 2006; see also Zhang et al., 2008).

Any systematic effect on microsaccade rate will result in different degrees of MLR overlap between conditions. In the time domain, this will change the ERP waveshape, shift scalp topographies, bias dipole estimates, and increase overall response variability (Gur et al., 1997). In the frequency domain, the MLR translated to increased spectral power in the alpha and theta band and was followed by several cycles of alpha ringing in Exp. 3. This indicates that microsaccades can influence time-frequency analyses also in frequency bands below gamma.

The specific impact of MLRs will depend on MLR amplitude, the size of any condition effect on microsaccade rate, and the electrode and time window under investigation: Because most microsaccades occur during the microsaccadic rebound and the MLR needs another 100 ms to reach its peak, MLRs will mostly influence late ERP components and their effect will be strongest at occipital and midcentral sites.

In the oddball task, microsaccades modulated the absolute ERP waveshapes and there was evidence for a condition-specific distortion at occipital electrodes. However, microsaccades did not substantially change the overall pattern of results in this experiment, except for an occipital shift in P300 topography as a function of condition, which might be erroneously interpreted as a condition-specific shift in P300 generators. The relative robustness of the P300 results relates to the fact that P300 oddball effects are among the largest in the ERP literature and have a maximum at parietal sites, where MLR effects were small in comparison. This is also the reason why in a previous report (Valsecchi et al., 2009), we did not observe microsaccadic modulations on P300, because we exclusively aggregated parietal electrodes over an earlier time window that was less affected by MLRs. Nevertheless, the present analyses suggest that modulations of experimental effects are likely if the stimulus is large and of high contrast, microsaccade probability varies between conditions, the ERP component of interest occurs late, and experimental effects are small.

Our results also complement the findings of Yuval-Greenberg et al. (2008): They suggest that microsaccadic muscle spikes – and the associated gamma-band artifacts – are inevitably present in the raw EEG; even under optimal conditions where (1) subjects fixate as precisely as they can, (2) a fixation point is continuously shown, and (3) microsaccades are only half the size of those observed by Yuval-Greenberg and colleagues.

Conclusions

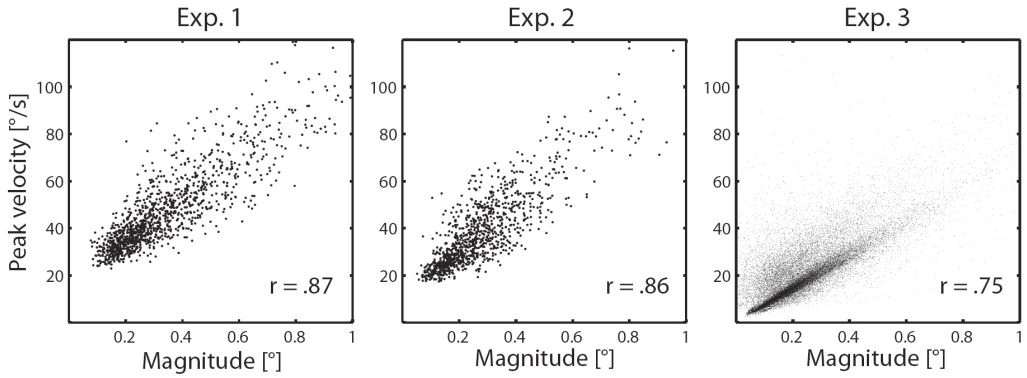
Because microsaccades occur frequently during any fixation task, consideration of their visual potentials should improve the signal-to-noise ratio of ERP data and the variance explained by single-trial models of EEG (e.g. brain-computer interfaces). Furthermore, it is important to stress that unlike the myogenic spike potential (Yamazaki, 1968), the MLR reflects genuine cortical activity and not an EEG-specific artifact. We therefore expect that occipital cortical responses from microsaccades are also frequently overlaid on magnetoencephalographic and possibly hemodynamic datasets. In summary, our results document the importance of simultaneous eye movement monitoring and the need to further understand the factors that influence fixational instability. Microsaccade-related brain potentials are both a tool to study visual perception during fixation and a neglected signal source in human neuroimaging.

Acknowledgements

The authors thank A. Pajkert, K. Schäfer, and K. Unger for assistance in data acquisition, A. Terzibaschian for assistance in data analysis, A. Schacht for providing face stimuli, and K. Mergenthaler and M. Rolfs for valuable comments. This work was supported by DFG Forschergruppe 868.

Supplementary Materials for Publication 1

Supplementary Figure S1.5

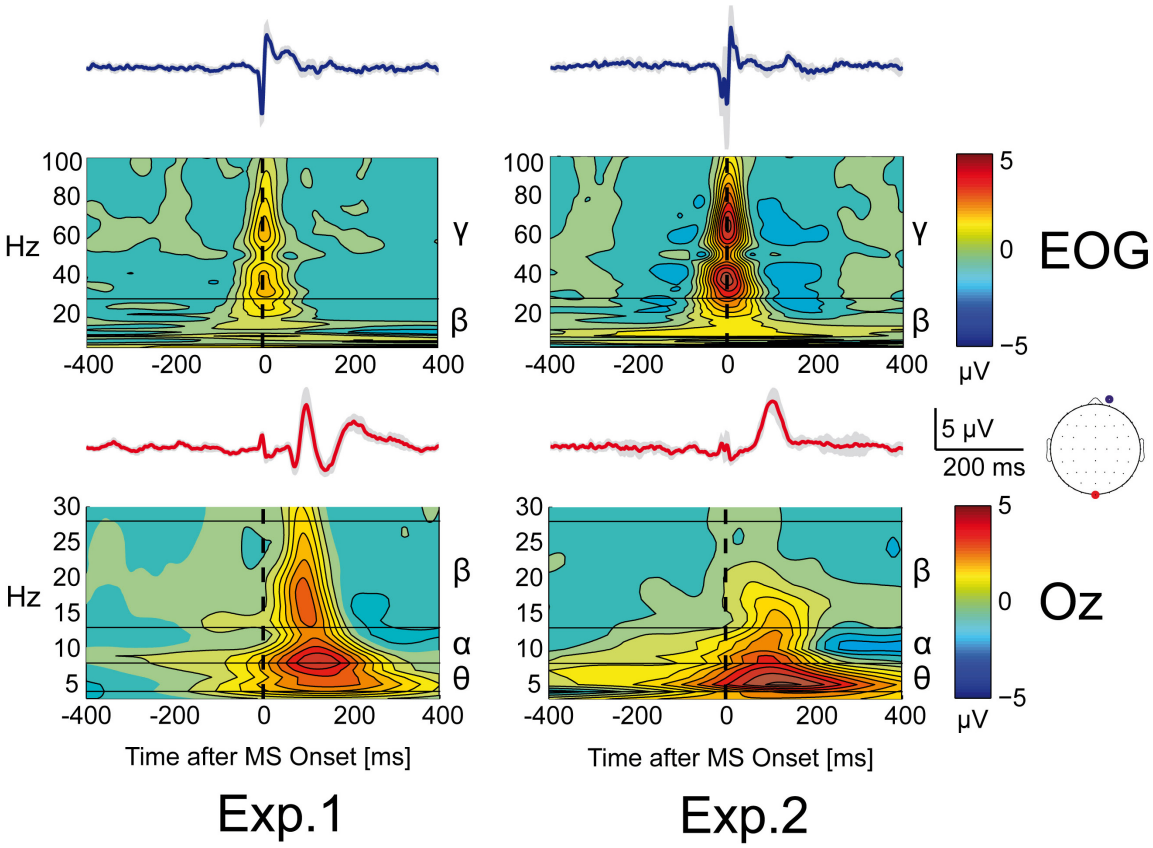


Magnitude-velocity relationship of microsaccades in the three experiments. The linear relationship ('main sequence', Zuber et al., 1965) is indicative of the fact that the events detected by the algorithm were microsaccades.

Methods for Supplementary Figure S1.2

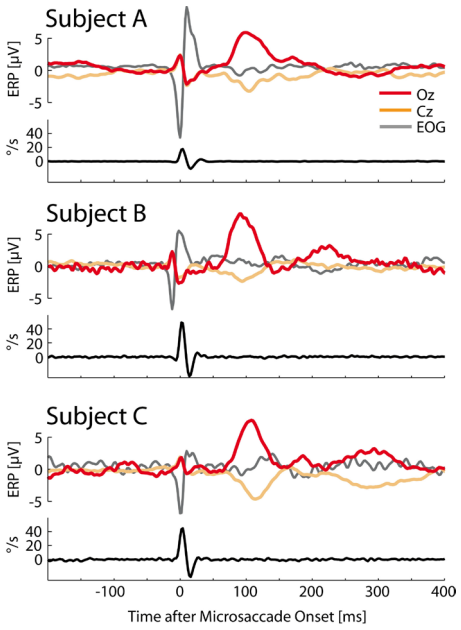
Time-frequency analyses were performed by convolving each microsaccade-locked EEG segment with a family of complex Morlet's wavelets (Tallon-Baudry and Bertrand, 1999) using the wavelet function in the BrainVision Analyzer Software (v1.05, Brain Products GmbH, Germany). Wavelet calculation was performed on a set of microsaccade-locked segments that was longer (from – 2000 to 1500 ms) and notch-filtered with a 50 ± 2 Hz (48 dB) band rejection filter to eliminate a line noise artifact emitted by the near-by eye tracking hardware. Wavelets were applied to center frequencies from 3 to 100 Hz in steps of 1 Hz. The constant ratio $m = F_0/\sigma_f$ (where F_0 is the wavelet's center frequency and σ_f its SD in the frequency domain) was set to $m = 12$ for the analysis of high frequencies (upper panels) and $m = 6$ for low frequencies (3-30 Hz, lower panels). Single-trial scalograms were baseline-corrected by subtracting at each frequency the mean activity from -1500 to - 1000 ms before microsaccade onset. An early baseline was chosen to avoid temporal smearing of microsaccade-related activity into the baseline at low frequencies (Herrmann et al., 2005). Time-frequency data was first averaged within each subject, and then collapsed across subjects.

Supplementary Figure S1.2



Grand mean ERP and time-frequency plots for microsaccade-related potentials in experiments 1 and 2. *Upper panels:* Data for the right infraorbital EOG electrode, where the microsaccadic spike potential (SP, visible in the averaged ERP trace) was largest. The wavelet transform was applied to individual microsaccade-locked segments and then averaged (see *Materials and Methods for Figure S1.2*). The transient SP translated to an increase in spectral power in the high beta and gamma band at movement onset. Because microsaccades occur with temporal jitter in each trial, microsaccadic SPs can mimic an increase in the power of "induced" (non-phase-locked) gamma band oscillations (Yuval-Greenberg et al., 2008). Horizontal lines indicate frequency band limits. The power reduction at 50 Hz is due to the notch filter. *Lower panels:* Data at occipital electrode Oz. The waveform of the microsaccadic lambda response (MLR) translated to a broadband increase in spectral power with a maximum in the theta and lower alpha band about 100 ms after microsaccade onset.

Supplementary Figure S1.3



Single subject averages for Exp. 2 (sustained face fixation). Microsaccade-related potentials are shown for Oz, Cz, and the right infraorbital EOG electrode. Lower traces show eye velocity; negative velocities represent movements against the predominant orientation of the microsaccade. In one of the subjects (subject B), the spike potential peaked already 10 ms before the detected movement onset in the eye track, causing a double spike in the grand-averaged data (shown in Figure 1.3).

Supplementary Figure S1.4

Comparison of stimulus-evoked and microsaccade-evoked potentials in the oddball experiment (Exp. 3). Data is shown for occipital electrode Oz. Shading indicates 95% between-subject confidence intervals. *Upper panel*: ERP time-locked to the onset of the red or green disc stimulus. The P1 component of the visual evoked potential (VEP) peaked after 124 ms, followed by the endogenous P300 component, which was also visible at occipital sites. *Lower panel*: ERP time-locked to the onset of microsaccades, detected during the trials of the oddball task. SP = spike potential. The microsaccadic lambda response (MLR) peaked after 136 ms. Scalp topographies are shown at the respective peak latencies of the P1 and MLR. Electrodes below the horizontal meridian are plotted outside the head perimeter. Note that the MLR, which frequently overlapped the stimulus-locked EEG epochs, was of similar amplitude as the VEP evoked by stimulus onset.

Materials & Methods for Figure S1.5: Face classification experiment

Subjects

Twelve healthy students (8 female, 19-35 years) participated after providing written informed consent. Subjects were different from those tested in Exp. 1-3 and naïve as to the purpose of the experiment.

Stimuli

Color portraits (7.5° × 8.5°) of 40 male or female persons (see Figure 1.3a) were used. The face of each person was shown with three emotional expressions (anger, happiness, or

neutral expression), leading to a set of 120 stimuli. Faces were presented on a 14 cd/m2 gray background at a monitor refresh rate of 120 Hz and a resolution of 1024x768 pixels. In contrast to Exp. 2, face stimuli did not include a fixation point. Presentation hardware was identical to Exp. 1 and 2.

Procedure

Subjects performed a speeded manual classification of the face's emotional expression. Responses were given with three keys, operated with the index, middle, and ring finger of the right hand. In each of four experimental blocks, all 120 stimuli were presented in random order. At the beginning of a trial, a 0.26° white fixation cross was presented on a gray screen for 1000 ms. It was immediately followed by the face, which remained on screen for 1350 ms. Subjects received standard written instructions to minimize blinks and eye movements while the stimulus was visible.

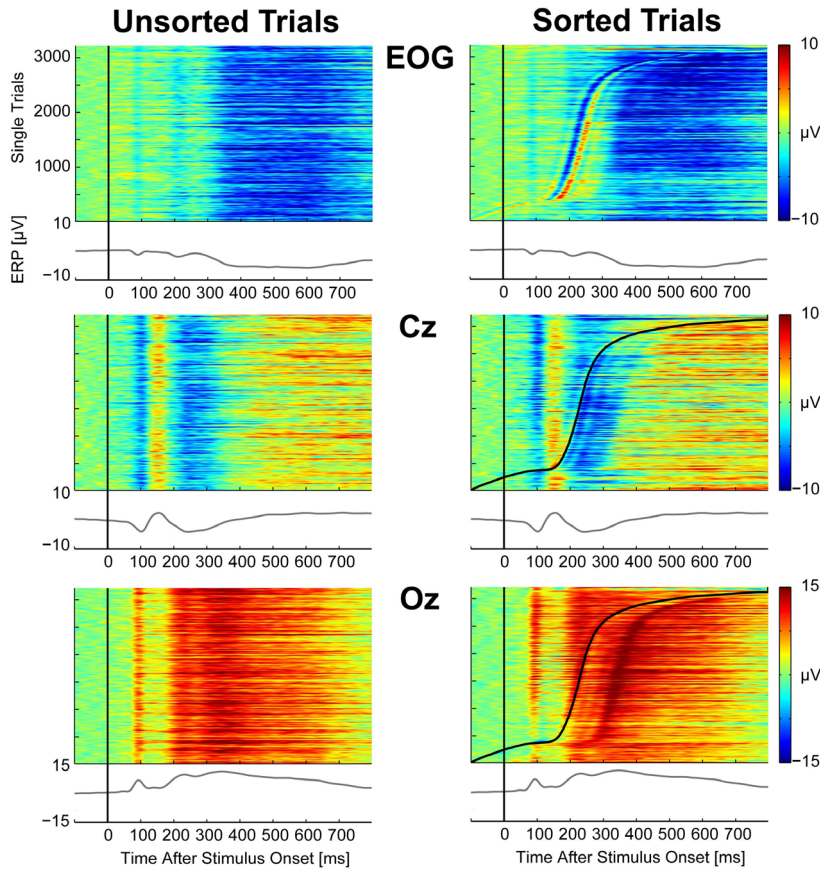
FEM and EEG recording

FEM were recorded binocularly at a rate of 500 Hz using the same eye tracker as in Exp. 1 and 2. Microsaccades and saccades were detected with the algorithm and parameters described for Exp. 1, with the additional constraint of binocularity (i.e. high-velocity movements were only classified as (micro)saccades if they occurred with temporal overlap in both eyes). The EEG recording setup was identical to Exp. 3. Offline, EEG channels were filtered with a bandpass from 0.1 to 30 Hz and re-referenced against the average of all channels.

Data analyses

EEG segments of 900 ms (-100 to 800 ms) were cut around each stimulus onset and baseline-corrected with a 100 ms pre-stimulus baseline. We rejected all segments with eye blinks or large saccades (> 3°) in the concurrent eye track. Additionally, an EOG-based rejection threshold was applied: All segments were rejected in which the horizontal or vertical bipolar EOG exceeded ±75 μV. The remaining segments (56%) were then sorted according to the latency of the first microsaccade or saccade detected in the eye tracking data of the respective trial. For visualization, trials were smoothed with a moving average across 20 adjacent trials after sorting.

Supplementary Figure S1.5



Impact of small saccades on stimulus-locked ERPs in a face classification experiment with large pictorial stimuli, long stimulus duration, standard fixation instructions, and no embedded fixation point (see *Materials and Methods for Figure S1.5*). Single-trial EEG segments from twelve subjects are shown. Time 0 indicates the onset of the face stimulus that required a manual choice reaction. Bottom panels of each plot show the stimulus-locked ERP (grey line) that is obtained by averaging at each time point ("vertically") across all trials. *Left column*: The impact of saccades is not evident when segments are plotted in random order. *Right column*: Same data, after sorting by the latency of the first microsaccade or saccade (black line) detected in each trial. Despite an EOG-based artifact rejection, at least one saccade was observed in 95% of the segments, with a median magnitude of 1.58° (±0.41). The muscle SP is visible in the mean signal from the left and right horizontal EOG electrode ("EOG"). Plots for electrodes Cz and Oz show how saccadic lambda responses alter the ERP morphology. For example, the negative ERP deflection at Cz between 200-300 ms can be partially attributed to microsaccade-evoked potentials. Similarly, at electrode Oz, the late positive complex (LPC) is increased by overlapping lambda responses.

2. Microsaccadic inhibition and P300 enhancement in a visual oddball task[11]

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Abstract

It has recently been demonstrated that the presentation of visual oddballs induces a prolonged inhibition of microsaccades. The amplitude of the P300 component in event-related potentials (ERPs) has been shown to be sensitive to the category (target vs. nontarget) of the eliciting stimulus, its overall probability, and the preceding stimulus sequence. In the present study we further specify the functional underpinnings of the prolonged microsaccadic inhibition in the visual oddball task, showing that the stimulus category, the frequency of a stimulus, and the preceding stimulus sequence influence microsaccade rate. Furthermore, by co-recording ERPs and eye movements, we were able to demonstrate that, despite being largely sensitive to the same experimental manipulation, the amplitude of P300 and the microsaccadic inhibition predict each other only weakly.

[11] published in 2009 in *Psychophysiology, 46*, 635-644

Introduction

During the last 10 years, the interest about eye movements during fixations has increased considerably. Due to the introduction of video-oculographic methods for the recording of eye movements, it is now possible to reliably identify microsaccades, which are fast (up to 300°/s) mainly conjugate eye movements occurring about once per second (Møller, Laursen, Tygesen, & Sjølie, 2002). Many relevant results have emerged. For example, it has been shown that microsaccades modulate the firing of neurons in the visual system (Leopold & Logothetis, 1998; Martinez-Conde, Macknik, & Hubel, 2000, 2002) by counteracting neural adaptation and the fading of peripherally presented stimuli during sustained fixation (Martinez-Conde, Macknik, Troncoso, & Dyar, 2006). This hypothesis is consistent with the finding that microsaccades become more frequent when the retinal displacement produced by slower fixational eye movements (i.e., drifts) is reduced (Engbert & Mergenthaler 2006). Microsaccades have also been found to play a role in the maintenance of correct visual fixation (Engbert & Kliegl, 2004; Liang et al., 2005; Mergenthaler & Engbert, 2007). Finally, there is growing evidence that the orienting of spatial attention biases the direction of microsaccades (Betta, Galfano, & Turatto, 2007; Engbert & Kliegl, 2003; Galfano, Betta, & Turatto, 2004; Laubrock, Engbert, & Kliegl, 2005; Laubrock, Engbert, Rolfs, & Kliegl, 2007; Rolfs, Engbert, & Kliegl, 2004, 2005; Turatto, Valsecchi, Tame`, & Betta, 2007; but confirmed on other high-speed fixational eye movements known as saccadic intrusions (Gowen, Abadi, Poliakoff, Hansen, & Miall, 2007).

Microsaccades also seem to be influenced by higher-level cognitive factors other than spatial attention. In his seminal work on fixational eye movements, Barlow (1952) described a reduction in the rate of microsaccades when participants were required to perform a demanding cognitive task. This was based largely on nonsystematic observations of the participants' behavior. However, recent works have confirmed that microsaccades are inhibited when participants encounter rare task-relevant visual stimuli, which have to be counted. Valsecchi, Betta, and Turatto (2007) measured the rate of microsaccades in a visual oddball task, which consisted of the serial presentation of rare target stimuli (oddballs) and frequent nontarget stimuli in random order. The authors found that the probability of microsaccades following the presentation of standard stimuli showed a biphasic time course, with an early inhibition phase peaking at 100–150 ms after stimulus onset and a later rebound phase peaking at 300–350 ms after stimulus onset. This stereotypical response has been widely observed in response to visual (Engbert & Kliegl,

2003; Galfano et al., 2004) and acoustic (Rolfs et al., 2005) stimuli, and is considered a subcortical oculomotor reflex possibly occurring at the superior colliculus level, at least in its inhibitory component (Engbert, 2006). However, Valsecchi et al. (2007) found that the inhibitory phase of the microsaccadic response was prolonged and the rebound almost abolished after the presentation of an oddball stimulus. This effect was observed both with peripheral and central stimuli and for different stimulus onset asynchronies, but it was absent when the oddballs were not task relevant. The authors suggested that the prolonged inhibition of microsaccades could be considered an index of the evaluation of task-relevant stimuli in the visual oddball paradigm. In a more recent study (Valsecchi & Turatto, 2007), the authors again found the prolonged inhibition of microsaccades in response to visual oddballs, while also showing, by using stimuli equiluminant with the background, that a cortical visual pathway can support the modulation of microsaccade rate in response to both oddball and standard stimuli. Recently, Valsecchi and Turatto (2009) showed that oddball stimuli induce a prolonged inhibition of microsaccades also in the auditory modality, a finding consistent with the hypothesis that this effect is an index of later and nonmodality-specific stages of stimulus processing.

Oddball paradigms have been extensively used in psychophysiological studies for four decades (e.g., Donchin & Coles, 1988; Johnson, 1988; Näätänen, Gaillard, & Mäntysalo, 1978). A specific response to oddball or infrequent stimuli has been observed in several peripheral measures, such as galvanic skin response (e.g., Bahramali et al., 1997; Lim et al., 1999), heart rate (e.g., Lyytinen, Blomberg, & Näätänen, 1992; Simons, Graham, Miles, & Balaban, 1998), and pupillary dilation response (Friedman, Hakerem, Sutton, & Fleiss, 1973).

A large amount of evidence has been collected with respect to the P300 component in the event-related brain potential (ERP). The P300 is a centro-parietal positivity peaking at around 300 ms after stimulus onset. This component has been considered an index of stimulus categorization (Donchin & Coles, 1988; Kok, 2001; Kutas, McCarthy, & Donchin, 1977; Verleger, 1988) and has been shown to be sensitive to both the stimulus category, that is, targets induce a higher-amplitude P300 than nontargets, and its overall, a priori frequency, that is, the less frequent a stimulus, the larger the elicited P300 (e.g., Duncan-Johnson & Donchin, 1977). P300 amplitude is also modulated by stimulus sequence (Jentzsch & Sommer, 2001; Squires, Wickens, Squires, & Donchin, 1976), with disruptions of runs of stimulus repetitions or alternations eliciting larger P300 amplitudes than continuations of such runs. The sequence-based enhancement of P300 amplitude can be

dissociated from the effect of overall stimulus frequency (Duncan-Johnson & Donchin, 1977).

Hence, microsaccadic inhibition and P300 enhancement are both observed in response to rare targets in visual oddball paradigms. However, it remains to be shown whether microsaccadic inhibition is also sensitive to target effects and stimulus sequence as is P300 amplitude. To answer these questions and to establish whether the similarity between the two measures goes beyond the sensitivity to the same experimental manipulations, we conducted a visual oddball experiment orthogonally manipulating stimulus frequency and stimulus category while simultaneously recording eye movements and ERPs. If a functional relationship exists between microsaccadic inhibition and P300 enhancement, we expected to find effects of stimulus category, stimulus frequency, and stimulus sequence on both measures. Moreover, if the two phenomena are directly related they could predict each other.

Methods

Participants

Thirteen young adults took part in the experiment. One participant's data were discarded from analysis because of the presence of blinks in more than 50% of the epochs. The mean age of the remaining 12 participants was 25.6 years; 9 were women. All participants reported normal visual acuity, showed normal color vision according to the Ishihara Color Vision Test (Ishihara, 2003), and were right-handed according to the Edinburg Inventory (minimum score = 64; Oldfield, 1971). Two of the authors (M.V. and O.D.) took part in the experiment, whereas all other participants were naïve as to the purpose of the study. The inclusion of two nonnative participants in the sample is potentially a confound, but its impact should be limited given that little voluntary control is expected on microsaccadic frequency and P300. All participants gave informed consent and were remunerated either with 7€ per hour or course credits.

Stimuli

Stimuli were red or green disks (2.04° in diameter), with a white fixation dot (0.481 in diameter) at the center. To enhance the physical similarity between target and nontarget stimuli and to control for intensity effects, the luminance of the red and green colors was matched for each participant using 25-Hz flicker fusion (Ives, 1912). The background was black during the entire experiment. Stimuli were presented on a 19-in. LG Flatron 915FT

CRT monitor at a refresh rate of 100 Hz and a viewing distance of 75 cm. Stimulus duration was 100 ms, inter stimulus interval was 900 ms, and the fixation point remained visible during the interstimulus interval. Stimulus presentation was controlled using *Presentation* software (Neurobehavioral Systems, Inc., San Francisco, CA).

Experimental Procedure

Participants sat in a dimly illuminated, acoustically and electrically shielded cabin. The experiment was divided into three conditions. In each condition, 500 stimuli were presented in random order. Participants had to silently count the stimuli matching the target color, which alternated between participants, and had to fixate the white dot while minimizing eyeblinks during the experimental sessions. After each block of 100 stimuli, participants reported the number of stimuli and were allowed to rest. Forty additional stimuli were presented in a practice block before each experimental condition. In the first condition, 50% of the stimuli were targets, whereas in the following two conditions the frequency of targets could be either 20% or 80% (the order of the last two conditions was alternated across participants). The 50% condition was always run first in order to avoid possible carryover effects, that is, participants might otherwise have implicitly adopted a biased expectation about the global stimulus frequency from the previous condition.

Eye-Movement Recording and Microsaccade Detection

Eye movements were recorded monocularly, with an iViewX Hi-Speed infrared eye-tracker (SensoMotoric Instruments, Teltow, Germany). Movements of the head were limited by the eye tracker's built-in chin and forehead rest. Recording was from the right eye, though viewing was binocular. The system had a sampling frequency of 238 Hz, a tracking resolution of < 90 s-arc and an absolute gaze position accuracy of up to 0.2°. A standard 9-point calibration was performed before the beginning of each block of 100 stimuli. Fixation was checked after every 10 trials. If the gaze was found outside of a 2.04° × 2.04° square centered around the fixation point, the experiment was interrupted and the system recalibrated.

Microsaccades were detected using the algorithm introduced by Engbert and Kliegl (2003). The algorithm was applied to epochs ranging from 150 ms before stimulus presentation to 1050 ms after stimulus presentation. Microsaccades were defined as parts of the eye position trace where velocity (calculated with a 5-point moving window) exceeded a combined threshold for the vertical and horizontal component equal to six times the standard deviation of the velocity profile within the epoch. Minimum allowed duration was

four samples (16.8 ms) and maximum allowed peak velocity was 200°/s. Additionally, microsaccades starting less than four samples after the previous microsaccade were rejected. Epochs containing blinks or saccades with amplitudes greater than 11 were discarded from analyses. Microsaccades were included in the analysis regardless of their spatial orientation.

Electrophysiological Recording

The electroencephalogram (EEG) was recorded from 40 Ag/AgCl electrodes on the scalp and around the eyes. Thirty-four of the electrodes were mounted in an elastic electrode cap (Electrocap International Inc., Eaton, OH) at positions Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, FT9, FC5, FC1, FC2, FC6, FT10, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO9, O1, Oz, O2, PO10, and Iz (American Electroencephalographic Society, 1994). Foam cushions were fitted to the participant's forehead to avoid direct pressure on the frontal electrodes. Six external electro-oculogram (EOG) electrodes were affixed at the outer canthi of the left and right eyes, below each eye, and on the left and right mastoids. An electrode at AFz was used as ground. All impedances were kept below 5 kΩ. A Brainamp DC amplifier (Brain Products GmbH, Munich, Germany) digitized the data at a sampling rate of 250 Hz, and a bandpass from DC to 70 Hz. Data was recorded with a PC running BrainVision Recorder Software (Brain Products GmbH). All channels were initially referenced to the left mastoid (A1) and converted to average reference off-line. Synchronization between EEG and eye tracker was achieved via TTL pulses sent from the stimulus presentation PC to both systems on every trial. The co-registration setup used in the present study has previously been applied and evaluated in several psycholinguistic experiments on reading (Dimigen et al., 2006).

Data Analysis

The eye tracking data and the ERP data were first analyzed separately. In particular, we extracted three measures of microsaccadic inhibition, that is, amplitude of the peak microsaccade rate, latency of the peak microsaccade rate, and rate of microsaccades in a specific time window of interest (WOI), and one measure of P300 amplitude, that is, the average voltage at electrodes P3, Pz, and P4 between 200 and 500 ms. Repeated measures analyses of variance (ANOVAs) with Stimulus Category (target vs. nontarget) and Stimulus Frequency (20%, 50%, or 80%) as factors were performed on each of the different measures.

Subsequently, we looked for sequence effects on the microsaccade rate in the time WOI and on P300 amplitude. We identified continued and discontinued sequences of stimulus repetitions, which are known to generate different P300 amplitudes, in the 50% stimulus frequency condition, and we performed repeated-measures ANOVAs with Stimulus Category and Sequence as factors.

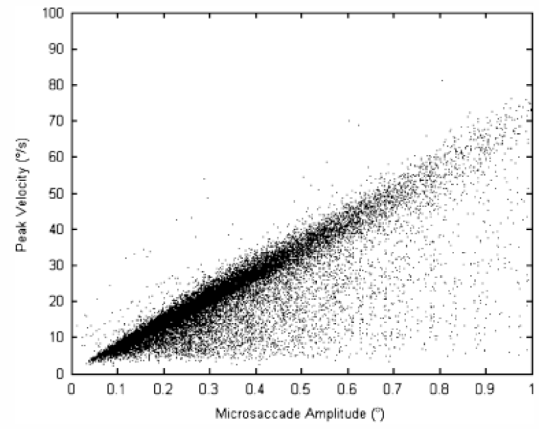
Finally, to explore the relationship between microsaccades and P300, within the 50% frequency target trials, we investigated whether the presence of a microsaccade in the time WOI and the P300 amplitude within a trial were predictive of each other. Greenhouse–Geisser corrected degrees of freedom and p values are reported where applicable.

Results

Counting Task

The participants were highly accurate in counting the target stimuli. The mean absolute counting error was 1.19% in the experimental condition with 50% targets, 0.91% in the condition with 20% targets, and 0.95% in the condition with a target frequency of 80%. No counting errors occurred in 77.09% of the reports. The counting data were not statistically analyzed.

Figure 2.1



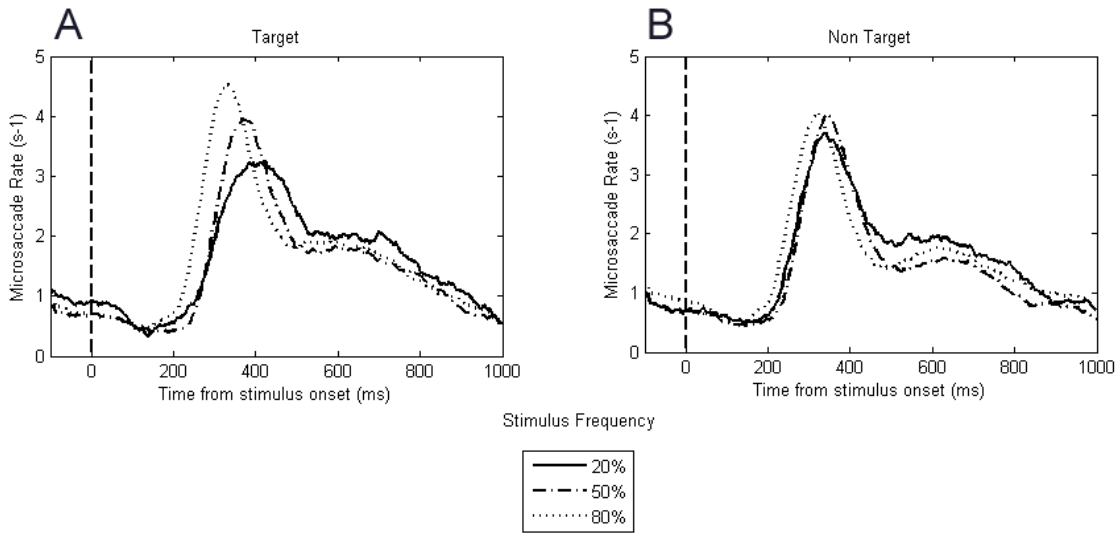
Microsaccade peak velocity as a function of microsaccade amplitude (defined as the maximum displacement between any two points along the movement trace). A clear linear relationship (main sequence) is evident.

Microsaccade Rate: Stimulus Category and Frequency Effects

The minimum number of epochs for each cell of the experimental design (i.e., for each combination of participant, stimulus frequency, and stimulus category) was 36. The relationship between peak velocity and microsaccade amplitude, defined as the maximum displacement between any two points along the movement trace, is depicted in Figure 2.1. The linear relationship (main sequence) is indicative of the fact that the events detected by the algorithm are microsaccades (Zuber, Stark, & Cook, 1965).

The evolution of microsaccade rate in response to target and nontarget stimuli is depicted in Figure 2.2, separately for the three stimulus frequency levels (20%, 50%, and 80%). The rate was calculated in a sliding time window of 100 ms, moving in steps of 4.2 ms (i.e., the maximum temporal resolution allowed by the sampling frequency of the eye tracker). The plots were constructed for each participant, stimulus frequency, and stimulus category, and subsequently averaged across participants.

Figure 2.2



Evolution of microsaccade rate in response to target (**A**) and nontarget (**B**) stimuli for the three levels of stimulus frequency (20%, 50%, and 80%). The rate has been calculated in a 100-ms-wide time window moving in 4.2-ms steps.

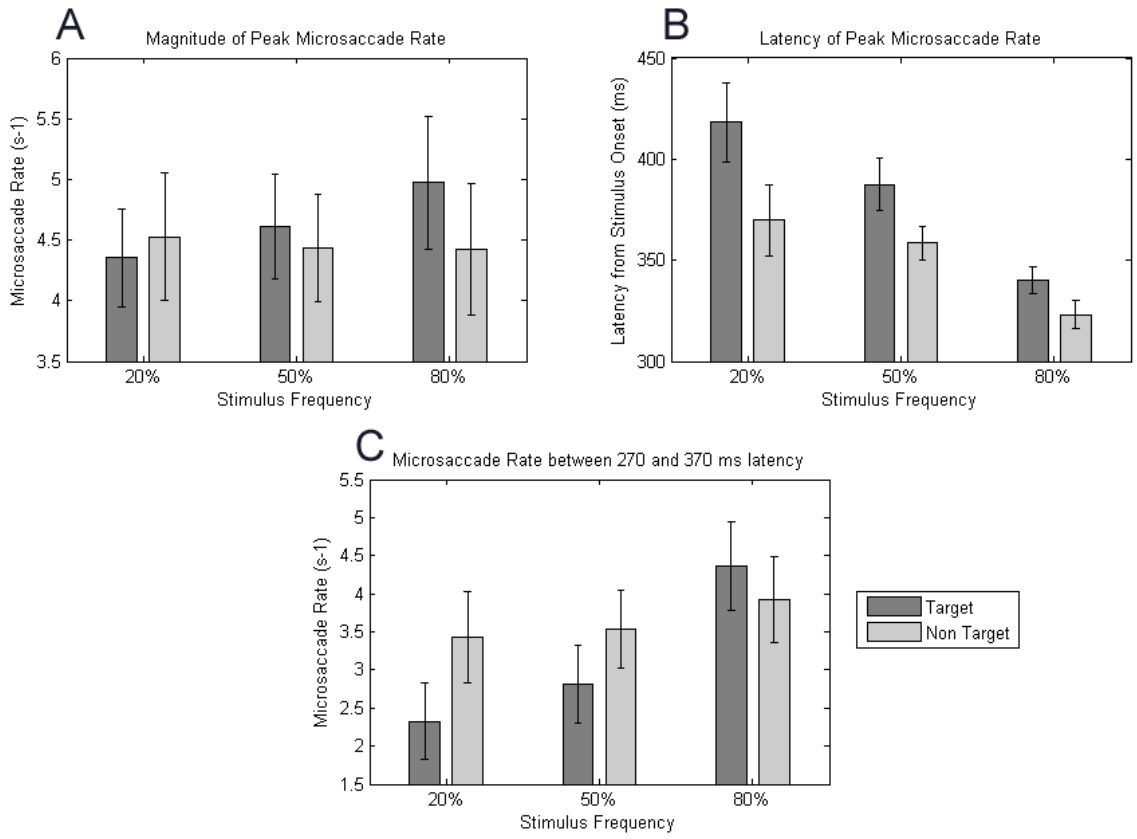
To ensure that the visual stimuli induced a reliable inhibition of microsaccades, we first identified the time point at which the minimum microsaccade rate was reached for each stimulus category and stimulus frequency. The average latency of the inhibition peak across stimulus category and stimulus frequency was 138.7 ms. The microsaccadic rates in two

100-ms bins, the first one centered on 0 ms latency (i.e., stimulus onset) and the second one centered on 138.7 ms latency (i.e., the inhibition peak), were analyzed in a three-way ANOVA with Bin (0 vs. 138.66 ms), Stimulus Category, (Target vs. Nontarget), and Stimulus Frequency (20%, 50% or 80%) as factors. The main effect of Bin was significant, $F(1,11) = 12.05$, $p<.006$, showing the overall presence of an inhibition effect. The Bin × Stimulus Category and the Bin × Stimulus Frequency interactions were not significant (both $ps>.05$).

Of central interest for the present study, however, was the later rebound in microsaccade rate. A peak in microsaccade rate was reached in all conditions between 300 and 500 ms after stimulus onset. The magnitude of the peak rate and its latency seemed to be modulated by stimulus frequency and stimulus category, and this modulation was more evident in the case of target stimuli. In particular, with increasing target frequency, the amplitude of the peak microsaccade rate seemed to increase, whereas the latency of the peak seemed to decrease.

This observation was confirmed by a statistical analysis. The magnitude of the peak microsaccade rate and its latency could be identified for each participant as the earliest point where the maximum value in microsaccade rate was reached in the single participant equivalent of the plots in Figure 2.2. Additionally, we calculated the microsaccade rate in a 100-ms time WOI centered on the latency of the peak microsaccade rate observed in response to the most frequent nontarget stimuli. The center of the WOI was set at 320 ms after stimulus onset according to the grand averages in Figure 2.2B (also see Valsecchi et al., 2007). A separate 3 × 2 ANOVA with Stimulus Frequency (20%, 50%, or 80%) and Stimulus Category (target vs. nontarget) as factors was applied to each of the three measures.

Figure 2.3



Mean magnitude of peak microsaccade rate (**A**), mean latency of peak microsaccade rate (**B**), and mean microsaccade rate in the time WOI between 270 and 370 ms after stimulus onset (**C**). Error bars are between-participant standard errors of the mean.

In the case of the magnitude of peak microsaccade rate (Figure 2.3A), we did not observe a significant effect of Stimulus Category and Stimulus Frequency (both Fs<1), but their interaction was significant, $F(1.59,17.55) = 3.95$, $p<.046$. Post hoc tests were performed separately for the two stimulus categories. In the case of target stimuli there was a nonsignificant trend for the magnitude of peak microsaccade rate to increase as a function of the stimulus frequency, $F(1.46,16.04) = 3.05$, $p<.088$, whereas the peak microsaccade rate was unaffected by stimulus frequency in the case of nontargets, $F(1.55,17.05)<1$.

The same analysis was applied to the latency of the peak microsaccade rate (Figure 2.3B) revealing significant effects of Stimulus Category, $F(1,11) = 33.87$, $p<.001$, and Stimulus Frequency, $F(1.26,13.95) = 12.10$, $p<.002$, whereas their interaction was only marginally significant, $F(1.55,17.07) = 3.14$, $p = .079$. The latency of the peak microsaccade rate was

shorter for nontargets and decreased as the stimulus frequency increased. At least numerically, the effect of stimulus frequency seemed to be stronger in the case of targets as compared to nontargets.

Stimulus Frequency had a significant effect also on the microsaccade rate in the time WOI, $F(1.57,17.34) = 10.37$, $p<.002$ (Figure 2.3C), whereas the effect of Stimulus Category was not significant, $F(1,11) = 2.62$, $p = .134$. However, the interaction between the two factors was significant, $F(1.74,19.19) = 21.62$, $p<.001$. Post hoc tests were performed separately for the two stimulus categories. The rate of microsaccades in the time window centered at 320 ms after stimulus onset increased as a function of Stimulus Frequency in the case of target stimuli, $F(1.54,17) = 21.20$, $p<.001$, whereas the effect was not significant in the case of nontargets, $F(1.69,18.55) = 1.49$, $p = .249$).

This interaction of Stimulus Frequency and Stimulus Category shows that rare stimuli compared to frequent stimuli elicited a stronger microsaccadic inhibition in the WOI only if they were targets, that is, if they needed to be counted.

P300: Stimulus Category and Frequency Effects

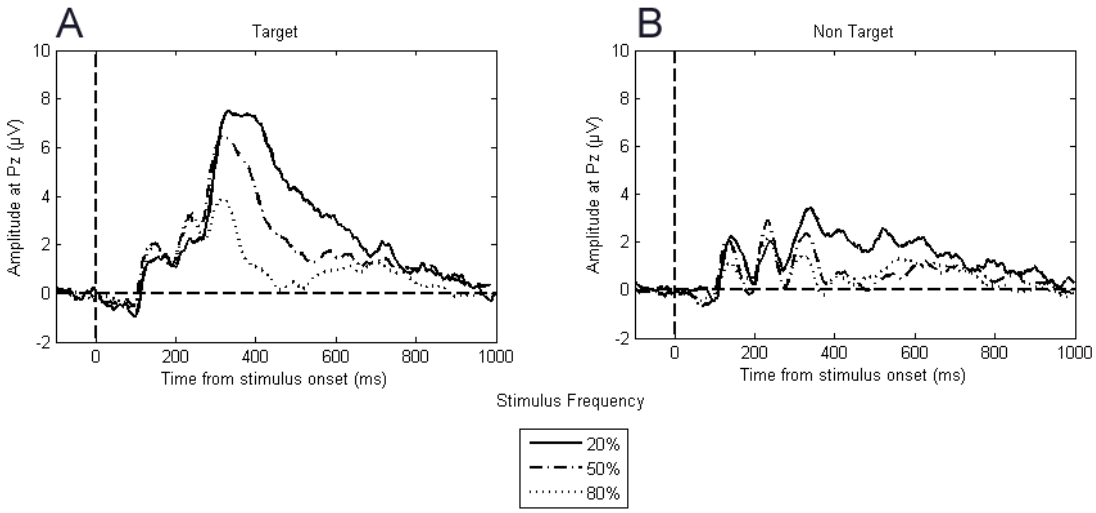
EEG data were segmented into epochs extending from 100 ms before stimulus onset to 1000 ms after stimulus onset and baseline corrected by subtracting for each channel the mean voltage in the 100-ms prestimulus interval. ERP analysis was conducted only on epochs that had not already been discarded from the microsaccadic analysis, that is, where neither blinks nor saccades longer than 11 were detected. Furthermore, we discarded epochs where drift artifacts (defined as absolute voltage values in the epoch exceeding 100 mV after baseline correction or a voltage difference between any two sampling points in the channel greater than 150 mV) were detected. The minimum number of epochs for each cell of the experimental design (i.e., for each combination of participant, stimulus frequency, and stimulus category) was 35. The grand average of the voltage amplitude at electrode Pz in response to target and nontarget stimuli is depicted in Figure 2.4, separately for the three stimulus frequency levels (20%, 50%, and 80%). As in the case of microsaccade rate, there was a clear modulation of the waveform by stimulus frequency, and this seemed to be particularly evident in the case of target stimuli.

We chose to use the average voltage at electrodes P3, Pz, and P4 between 200 and 500 ms latency as a measure of P300 amplitude for statistical analysis. This choice was corroborated by the observation in the scalp topographic maps (not presented) that in this

time window the experimental manipulations most strongly affected the voltage at centroparietal electrodes, which is typical of this paradigm.

Moreover, a control analysis showed that voltage at these electrodes is unlikely to be contaminated by corneoretinal artifacts (e.g., Gratton, 1998) due to microsaccades. To estimate the corneoretinal artifact introduced by microsaccades, we classified them as either leftward or rightward oriented according to the horizontal movement component, because the majority of microsaccades are horizontally oriented. A segment of EEG was then cut around the onset of each microsaccade in the oddball experiment and baseline corrected with a 100-ms pre-microsaccade baseline. The mean voltage at the horizontal EOG electrodes (in a 100-ms interval following microsaccade onset) was used as an estimate for the corneoretinal artifact generated by microsaccades. The grand mean difference between the two electrodes (i.e., the bipolar-referenced EOG, left minus right electrode) in this interval was 1.74 mV for leftward-oriented microsaccades and -2.08 mV for rightward-oriented ones. The fraction of artifact that propagates from the horizontal EOG to centroparietal electrode Pz has been estimated by Picton et al. (2000; see their Table 1) as 0.028 and 0.024 for leftward and rightward horizontal saccades, respectively. Therefore, a maximum possible distortion of around ± 0.05 mV was expected at Pz. Furthermore, the distribution of microsaccadic direction in our experiment was quite symmetrical; around 50.1% of the microsaccades were rightward oriented. The actual distortion was therefore even smaller, due to the cancellation of artifacts from leftward- and rightward-oriented microsaccades in the averaging process.

Figure 2.4



Evolution of ERP amplitude at Pz in response to target (**A**) and nontarget (**B**) stimuli for the three levels of stimulus frequency (20%, 50%, and 80%).

A two-way ANOVA with Stimulus Frequency and Stimulus Category as factors revealed significant main effects of Stimulus Category, $F(1,11) = 61.94$, $p<.001$, and Stimulus Frequency, $F(1.58,17.48) = 29.14$, $p<.001$, on P300 amplitude. The two factors also interacted significantly, $F(1.36,14.97) = 7.87$, $p<.009$. The effect of Stimulus Frequency was more pronounced for target than for nontarget stimuli. Nonetheless, post hoc tests indicated that the frequency effect was significant for both targets, $F(1.38,15.18) = 24.7$, $p<.001$, and nontargets, $F(1.81,19.91) = 7.51$, $p<.005$.

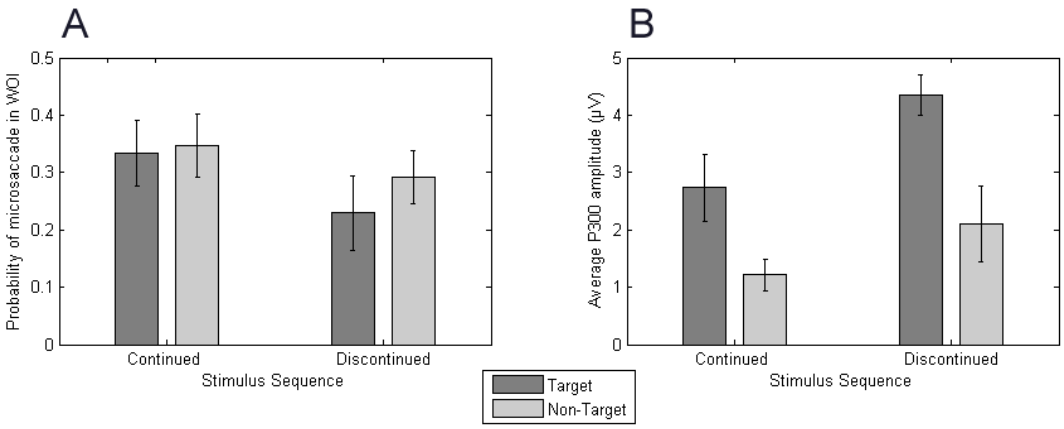
The pattern of ERP results was similar to the one we observed for microsaccades, with P300 amplitude affected by the interaction of stimulus frequency and category. The main difference between the two measures was that targets elicited a larger P300 amplitude compared to nontargets, whereas the target effect was not significant on microsaccadic rate. Notice that P300 amplitude decreased as a function of stimulus frequency, whereas the rate of microsaccades in the corresponding time window showed the opposite pattern, that is, it was higher for more frequent stimuli.

Sequence Effects

Sequence effects on microsaccade rate and P300 amplitude were analyzed only in the case of the 50% stimulus frequency condition, where all sequences of a given order were equiprobable. We analyzed the two fourth-order sequences (i.e., based on the type of the

current stimulus and of the preceding three; see Squires et al., 1976), which are expected to generate the lowest and the highest P300, respectively. "Continued" sequences, that is, sequences constituted by four repetitions of the same stimulus, induce the lowest P300 in response to the current stimulus, whereas "discontinued" sequences, that is, sequences where the current stimulus is preceded by three stimuli of the other type, induce the highest P300 (Jentzsch & Sommer, 2001; Squires et al., 1976).We excluded epochs that contained artifacts (ocular or other) or an interruption of the stimulus sequence, that is, a pause between blocks of trials or a recalibration of the eye tracker. The average minimum number of epochs for each participant, stimulus type, and sequence in this subset of data was 14. This number of trials was not sufficient to precisely identify peaks of microsaccade rate; consequently, we used the presence or absence of at least one microsaccade in the time WOI between 270 and 370 ms after stimulus onset as an index of microsaccadic inhibition. The mean values of the two measures for these two sequences are plotted in Figure 2.5. The pattern of modulation appeared to be opposite in the two measures, and the modulation was apparently stronger for the P300 measure.

Figure 2.5



Sequence effects on the probability of execution of a microsaccade in the time WOI (between 270 and 370 ms after stimulus onset) (**A**) and on the amplitude of the P300 (average ERP amplitude at P3, Pz, and P4 between 200 and 500 ms after stimulus onset) (**B**). The plots refer to the stimuli presented in the 50% frequency condition. "Continued" indicates a sequence of four identical stimuli and "Discontinued" indicates a sequence with three identical stimuli followed by a different one (the current stimulus). Error bars are between-participants standard errors of the mean.

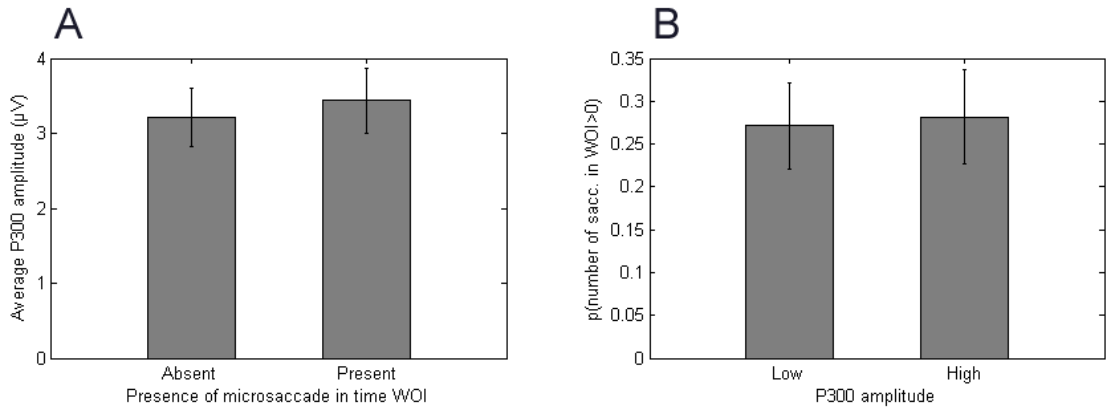
A two-way ANOVA of microsaccade rates with Stimulus Category (target vs. nontarget) and Sequence (continued vs. discontinued) as factors and the probability of occurrence of at least one microsaccade in the WOI as the dependent variable yielded a significant effect of the factor Sequence, $F(1,11) = 6.00$, $p<.032$, whereas the effect of the factor Stimulus Category and the interaction were not significant (both $Fs<1$). The same analysis was applied on the P300 measure and yielded a significant effect of the factor Sequence, $F(1,11) = 10.15$, $p<.009$, and Stimulus Category, $F(1,11) = 30.56$, $p<.001$, whereas their interaction was not significant ($F<1$). Once again, when the P300 was higher in amplitude for the discontinued sequences, the probability of occurrence of a microsaccade in the time WOI was lower. In addition, the P300 amplitude for target stimuli was higher as compared to nontargets, whereas no significant difference was found for the measure of microsaccadic inhibition.

The present analysis showed that sequence effects were evident in microsaccades as well as ERPs. In particular, discontinued sequences elicited a stronger microsaccadic inhibition and a larger P300 amplitude compared to continued sequences.

Relation between Microsaccadic and P300 Effects

To investigate whether our measures of microsaccadic inhibition and P300 are functionally related, we addressed whether the two measures are predictive of each other at the trial level. In particular, we checked whether the observation of at least one microsaccade in the time WOI was predictive of the P300 amplitude. To this purpose, for each participant and among the subset of target trials from the 50% frequency condition, we identified the epochs in which at least one microsaccade was observed in the time WOI and epochs in which no microsaccade was observed in the same time window. This subset was chosen because we had enough trials, the amplitude of P300 to targets was large enough to allow its detection on single trials, and because all stimulus sequences occurred with the same probability. The minimum number of saccade-present epochs for each participant was 79; the minimum number of saccade-absent epochs for each participant was 12. A paired t test showed that the amplitude of P300 was not significantly higher in saccade-absent epochs than in saccade-present epochs, $t(11) = 1.50$, $p = .161$ (see Figure 2.6A).

Figure 2.6



A. Average P300 amplitude in 50% frequency target epochs as a function of the presence of at least one microsaccade in the time WOI between 270 and 370 ms after stimulus onset. **B.** Average probability of observing at least one microsaccade in the time WOI between 270 and 370 ms after stimulus onset in 50% frequency target epochs as a function of P300 amplitude (median split classification). Error bars are between-participants standard errors of the mean.

We also conducted the converse analysis, that is, in the same whether the measure of P300 was predictive for the execution of a microsaccade independently of stimulus frequency and stimulus category. We performed a median split of the subset of trials based on the amplitude of P300 (average voltage at Pz, P3, and P4 between 200 and 500 ms after stimulus onset). This analysis yielded a minimum number of 90 epochs per participant and P300 amplitude bin (high vs. low). A paired t-test showed that the probability of observing at least one microsaccade in the time WOI was not significantly lower in the high-P300 epochs than in the low-P300 epochs, $t(11) = 0.69$, $p = .51$ (see Figure 2.6B).

Discussion

Several studies in the last decade have shown that microsaccades can be used as a tool to investigate the state of the cognitive system (see Engbert, 2006). In particular, Valsecchi et al. (2007) showed that the rate of microsaccades presents a prolonged inhibition when a rare target is encountered in a visual oddball task.

We propose that the microsaccadic inhibition is a new tool to investigate the brain's response in the oddball task, along with the other peripheral measures that have been studied in the past decades (e.g., Bahramali et al., 1997; Friedman et al., 1973; Lyytinen et al., 1992).

An enhancement of P300 amplitude is also commonly observed in response to visual oddballs (Hermann & Knight, 2001). The amplitude of the P300 component is sensitive to the sequence of the stimuli preceding the upcoming one (Duncan-Johnson & Donchin, 1977; Jentzsch & Sommer, 2001; Squires et al., 1976), so that stimuli discontinuing the preceding sequence elicit a higher P300.

Category/Frequency Effects on Microsaccades

The first aim of the present study was to establish whether the prolonged inhibition of microsaccades that was observed by Valsecchi et al. (2007) was due to target effects, to frequency effects, or to a combination of both. To answer this question, we conducted a visual oddball experiment varying the frequency of targets, which was 20%, 50%, and 80% in different conditions. Given the fact that the rebound in the rate of microsaccades, which normally follows the inhibition peak after the presentation of a visual stimulus (e.g., Engbert & Kliegl, 2003; Galfano et al., 2004), was clearly recognizable in the single-participant plots, we were able to individuate three measures of microsaccadic inhibition. The first measure was the rate of microsaccades in the time window where the rebound in response to the most frequent nontargets was observed. The second measure was the latency of the rebound peak, and the third was its amplitude. The three measures were not equally sensitive to the experimental manipulations, but in general we observed a more pronounced inhibition of microsaccades in response to less frequent stimuli, and this effect was stronger for targets. Pure target effects were only observed for the latency of the rebound peak, whereas they were not significant for the other two measures.

Category/Frequency Effects on P300

Simultaneously with microsaccades, we also recorded ERPs. We found P300 amplitude to be larger for less frequent stimuli and for targets as compared to nontargets. Moreover, the P300 amplitude modulation by stimulus frequency was stronger for targets than for nontargets, a pattern of results that has been reported previously (e.g., Duncan-Johnson & Donchin, 1977; Potts, Patel, & Azzam, 2004) and that has been interpreted as a sign of attentional effects on stimulus processing (Kok, 2001). In other words, the rare targets would capture attention more than frequent and irrelevant stimuli. In the present study, microsaccadic inhibition and P300 were modulated in a coherent way by the task relevance and by the overall frequency of the stimuli, except for the fact that the target effect was less reliable for microsaccades, being significant only when the latency of the rebound peak was taken as a measure of microsaccadic inhibition.

Sequence Effects

We further addressed whether microsaccadic inhibition is influenced by the stimulus sequence. It has long been known that stimuli interrupting a series of identical stimuli induce a higher P300, irrespective of the a priori stimulus probability (Duncan- Johnson & Donchin, 1977; Jentzsch & Sommer, 2001; Squires et al., 1976). We replicated this observation in our P300 measure. Even when target and nontarget stimuli were equally probable overall, after three identical stimuli in a row, a stimulus change elicited a higher P300 than another repetition. This was true independently of whether the final stimulus was a target or not. Interestingly, the same pattern emerged in microsaccadic inhibition; the rate of microsaccades was more inhibited for discontinued than for continued repetition runs. As in the case of P300, the sequence effect on microsaccadic inhibition was observed both for targets and nontargets.

We can thus conclude that the overall probability and the preceding stimulus sequence determine both the amplitude of P300 and the extent of microsaccadic inhibition elicited by task-relevant stimuli. The somewhat weaker impact of task relevance on microsaccades as compared to stimulus frequency suggests that stimuli with an extremely low subjective probability could induce a microsaccadic inhibition even when task irrelevant. This, for example, could be the case of stimuli that are task irrelevant and are presented only once in the experiment and that are known to elicit the so-called novelty P300 (Courchesne, Hillyard, & Galambos, 1975; see Friedman, Cycowicz, & Gaeta, 2001). Moreover, we cannot exclude the possibility that sequence effects on microsaccadic inhibition are observed even when all stimuli are task irrelevant. However, this seems unlikely, because we have shown that, when participants passively view the stimuli, even overall rare stimuli have little effect on microsaccadic behavior (Valsecchi et al., 2007).

Notice that the ERP effects we observed are around two orders of magnitude greater than the maximum propagation of microsaccadic ocular artifacts expected at Pz. Therefore the impact of artifacts due to microsaccade-related movements of the retino-corneal dipoles on ERPs can be neglected as far as the measurement of P300 in oddball paradigms is concerned.

Comparison with Previous Studies

In the current study we confirmed that the flashing of a visual stimulus induces an inhibition of microsaccade rate with a latency between 100 and 150 ms, which is then followed by a rebound. It is interesting that the peak rate of microsaccades in response to

frequent nontarget stimuli in the present study was much higher than in the study of Valsecchi et al. (2007). This might depend on the different eye-tracking systems used in the two studies. In particular, the system used in the present study would only have supported binocular recording with a lower image quality and had a lower sampling frequency, being thus more noise sensitive. Nonetheless, we basically replicated the finding that standard stimuli induce a double-phase inhibition-rebound modulation in the absolute microsaccade rate and that the inhibition phase was longer and the rebound delayed in response to oddballs. In the study by Valsecchi et al. the rebound phase was almost abolished in response to oddball stimuli, whereas in the present study it was still clearly identifiable. We suspect that this might depend on two differences between the experimental procedures. First, the frequency of rare stimuli was raised from less than 10% in the Valsecchi et al. study to 20% in the present one, thus reducing the frequency effect. Second, in the present study the stimulus series were fully randomized, whereas Valsecchi et al. used pseudo-randomized series, in which at least six standard stimuli were presented between two oddballs. Hence, in the latter case the sequence effect should be much stronger than in the present case, leading to a more pronounced inhibition of microsaccades.

Relationship between Microsaccadic Inhibition and P300 Enhancement

To summarize, we showed that stimulus category, stimulus frequency and the previous stimulus sequence modulated the amplitude of P300 and that stimulus frequency and category interacted synergistically. The same effects were also observed as far as microsaccadic inhibition is concerned, with the following difference: A stimulus category effect was significant in the latency of the peak microsaccade rate, whereas the other measures of microsaccadic inhibition only showed a reliable stimulus frequency effect. As stated above, in all of the previous studies on microsaccadic inhibition in the oddball task, it was not possible to isolate the peak microsaccade rate in response to targets. Therefore, it is still an open question whether or to what extent the different measures of microsaccadic inhibition we used in this paradigm indexed different aspects of stimulus processing in the oddball task.

A final question we addressed was whether microsaccadic inhibition and the P300 shared more than the sensitivity to the same experimental manipulations. Within a specified cell of our experimental design, the microsaccadic behavior was not significantly predictive of the P300 amplitude and vice versa. This could be due to low statistical power, given the relatively small sample size, and to the unreliability of our measures. In any case, the relationship between microsaccadic inhibition and P300 enhancement deserves further

study, which could either reveal a relation that went undetected in our experiment or prove the independence of these two measures of the brain's response to rare targets in a visual oddball task.

The debate over the functional meaning of P300 has continued for four decades since this component was first reported (Sutton, Braren, Zubin, & John, 1965). In general, the most accepted view is the one that P300 is an index of context updating (Donchin, 1981; Donchin & Coles, 1988). This theoretical perspective considers P300 as a sign of the attentive restructuring of the stimulus representation in working memory when a new stimulus is encountered. Over the years, extensive evidence regarding the neural processes that could support the attention and memory operations related to P300 generation has been collected. Overall, the data seem compatible with the hypothesis that P300 reflects the neural inhibition that is functional to the focusing of activity on the processing of target stimuli (Polich, 2007). The inhibition model proposed by Polich is more specific in that it posits that the inhibition is revealed by a P3a when focal attention is summoned by rare distractors and revealed by a P3b when targets are evaluated in working memory. As far as the current evidence is concerned, we can propose that a similar mechanism also subtends the inhibition of microsaccades elicited by oddball stimuli; it is in fact clear that the inhibition of microsaccades is observed when a stimulus that requires a deeper restructuring of the task-related representation is encountered. However, in the present experiment we did not present rare distractors together with rare targets and frequent standards (three stimulus oddball paradigm), which is the experimental paradigm where P3a and P3b are more clearly distinguishable. Therefore, we cannot specify whether microsaccadic inhibition is more related to one of the two components.

A deeper knowledge of the neural system involved in the generation of microsaccades and in their inhibition could also probably be helpful in disentangling the differences between this oculomotor effect and the enhancement of P300 observed in response to infrequent targets in the oddball task. The neural generators of P300 have been studied using intracranial recordings (Halgren et al., 1995a, 1995b, Halgren, Marinkovic, & Chauvel, 1998; Roman, Brázdil, Jurák, Rektor, & Kukleta, 2005). A widespread network of cortical areas in the parietal, frontal, and temporal lobes and subcortical areas such as the hippocampus and the amygdala were identified as generators of P3-related ERPs. These findings have been confirmed by fMRI studies (Ardekani et al., 2002; Bledowski, Prvulovic, Hoechstetter, et al., 2004; Bledowski, Prvulovic, Goebel, Zanella, & Linden, 2004; Clark, Fannon, Lai, Benson, & Bauer, 2000; Stevens, Skudlarski, Gatenby, & Gore, 2000). As far as microsaccades are

concerned, there is indirect evidence that they are triggered by fixational activity within the superior colliculus, mainly derived from the observation that saccades, which are known to be elicited by stimulation of the superior colliculus (Robinson, 1972), feature a kinematic profile similar to the one of microsaccades (Zuber et al., 1965). Furthermore, it has been demonstrated that the inhibition of microsaccades in response to visual stimuli can be mediated by a cortical visual pathway sending afferences to the superior colliculus (Valsecchi & Turatto, 2007). Therefore we cannot exclude that some of the cortical generators of P300 could also be responsible for the prolonged inhibition of microsaccades. Overall, the current neurophysiological evidence does not indicate that the structures generating microsaccades and the P300 are anatomically segregated. It is well possible that the prolonged microsaccadic inhibition reflects inhibitory processes within cortical oculomotor areas, a mechanism similar to the one that has been proposed for P300 (Polich, 2007).

To conclude, we propose that P300 enhancement and prolonged microsaccadic inhibition are both indices of the brain's processing of subjectively rare relevant stimuli. Further research is needed to clarify the extent to which these two measures are functionally related.

3. Co-registration of eye movements and EEG in natural reading: Analyses & review[12]

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Abstract

Brain-electric correlates of reading have traditionally been studied with word-by-word presentation, a condition that eliminates important aspects of the normal reading process and precludes direct comparisons between neural activity and oculomotor behavior. In the present study, we investigated effects of word predictability on eye movements (EM) and fixation-related brain potentials (FRPs) during natural sentence reading. Electroencephalogram (EEG) and EM (via video-based eye tracking) were recorded simultaneously while subjects read heterogeneous German sentences, moving their eyes freely over the text. FRPs were time-locked to first-pass reading fixations and analyzed according to the cloze probability of the currently fixated word. We replicated robust effects of word predictability on EMs and the N400 component in FRPs. The data were then used to model the relation among fixation duration, gaze duration, and N400 amplitude, and to trace the time course of EEG effects relative to effects in EM behavior. In an extended *Methodological Discussion* section, we review four technical and data-analytical problems that need to be addressed when FRPs are recorded in free-viewing situations (such as reading, visual search, or scene perception) and propose solutions. Results suggest that EEG recordings during normal vision are feasible and useful to consolidate findings from EEG and eye-tracking studies.

[12] published in 2011 in the *Journal of Experimental Psychology: General, 140,* 552-572

Introduction

Reading is a complex cognitive task, unfolding at the same time at visual, attentional, lexicosemantic, and oculomotor levels. Comprehension requires the processing of visual input across a complex series of brief fixation pauses and saccadic eye movements as well as retrieving, updating, and integrating contents of memory. Current research on reading makes heavy use of two methods: recording eye movement (EMs) and event-related brain potentials (ERPs). Traditionally, these research methods have used different experimental protocols: In EM studies, subjects read sentences or paragraphs of text while their fixation position is monitored with an eye tracker. The durations, positions, and sequences of fixations are then used to make inferences about the underlying cognitive processes (Rayner, 1998). Procedures in these studies often resemble everyday reading without unusual task demands. In contrast, in ERP studies of reading, serial visual presentation (SVP) has typically been used to avoid saccade-related measurement artifacts in the electroencephalogram (EEG). In SVP, readers fixate the center of the screen while sentences are presented word by word at a predefined pace. ERPs are then time-locked to stimulus presentations.

In the present study, we demonstrate effects of a critical variable — the predictability of a word from the prior sentence context — in EMs and ERPs that were recorded simultaneously during left-to-right sentence reading. The predictability effect has figured prominently in both the EM- and the ERP-research traditions. Coregistration of EM and EEG may grant new perspectives on the relation between fixation time and single-trial EEG amplitude, as well as on the time course of predictability effects in both measures. Their simultaneous recording also raises several methodological problems to which we propose solutions. We argue that methodological advances in coregistration, as exemplified for reading in the present article, will also apply to other free viewing situations. In the following, we summarize (a) the rationale for focusing on word predictability effects, (b) the potential benefits of simultaneous recordings, (c) previous EEG studies in which some form of EM coregistration has been used, and (d) the methodological challenges that have limited the use of this technique.

Word Predictability in Reading

A word's predictability in the context of a given sentence is known to modulate both oculomotor behavior (e.g., Balota, Pollatsek, & Rayner, 1985; Kliegl, Grabner, Rolfs, &

Engbert, 2004; Rayner, Ashby, Pollatsek, & Reichle, 2004) and N400 amplitude (e.g., Dambacher, Kliegl, Hofmann, & Jacobs, 2006; Kutas & Hillyard, 1984). The well-established N400 component describes a negative-going ERP deflection, which is most pronounced around 400 ms after stimulus onset at centroparietal recording sites (Kutas & Hillyard, 1980). N400 amplitude is largest when a word violates the semantic context of a preceding sentence fragment, but is also larger for semantically correct words that are less predictable from the context. Because of its context sensitivity, N400 amplitude is thought to reflect the difficulty in retrieving conceptual knowledge associated with a word from memory, or in integrating it into the context of the sentence or discourse (Kutas, Van Petten, & Kluender, 2006). However, it remains controversial whether N400 effects reflect facilitated access to lexicosemantic features (Lau, Phillips, & Poeppel, 2008), a late post-lexical process of semantic context integration (Holcomb, 1993; Brown & Hagoort, 1993), or semantic inhibition (Debruille, 2007) and it is possible that multiple mechanisms contribute to the N400. Regardless of the theoretical viewpoint, the N400 provides information about the time course of semantic processing and its onset can be interpreted as an upper time limit for the initial access to word meaning. One aim of the present study was therefore to test for the existence of an N400 in a normal reading situation and describe its properties.

Predictability also figures prominently in current conceptualizations of reading from the perspective of eye movement control: Highly predictable words are skipped more frequently (e.g., Balota et al., 1985; Vitu, 1991; Drieghe, Rayner, & Pollatsek, 2005); fixations on them are shorter (e.g., Altarriba, Kroll, Sholl, & Rayner, 1996; Balota et al., 1985; Rayner et al., 2004); and high predictability of an upcoming word is associated with a longer fixation on the previous word (Kliegl, Nuthmann, & Engbert, 2006). Understanding the role of predictability in reading is also part of the broader question whether lexical processing is spatially distributed over several adjacent words, and whether lexicosemantic information – in addition to low-level visual and orthographic properties – is extracted from not-yet-fixated words in the parafovea (Kennedy, Pynte, & Ducrot, 2002; Kliegl et al., 2006; Kliegl, 2007; Rayner, Pollatsek, Drieghe, Slattery, & Reichle, 2007).

Potential Benefits of Simultaneous Recordings

From the perspective of ERP research, there is no doubt that SVP has proven itself to be extremely successful in studying the electrophysiological correlates of word recognition (Kutas et al., 2006). At the same time, it presents a strong simplification of the normal reading process, which differs in several ways from SVP: In normal reading, readers

determine how long each word is fixated and which word to fixate next. Words are therefore not inspected in a strictly serial fashion, but frequently skipped or fixated several times, and regressive saccades towards earlier words are common. Unlike SVP, normal reading allows for the preprocessing of upcoming words in parafoveal vision. At the same time, words are not always fixated at their center (as in SVP), but are often processed from non-optimal viewing positions near the word boundaries (Nuthmann, Engbert, & Kliegl, 2005). Another major difference concerns speed: While most ERP studies present words at stimulus-onset asynchronies of 400 to 1000 ms (i.e., 60-150 words per minute), average reading fixations last only 200-250 ms and reading speeds of 250 words per minute are common. Accordingly, new visual input is obtained at much higher rates than in most SVP experiments. Finally, SVP imposes secondary-task demands – to maintain fixation and refrain from blinking – absent in normal reading.

As a result of these differences, it is largely unknown to what extent SVP results apply to normal reading. There have been several approaches to improve the ecological validity of SVP. One is to present words at speeds that are very fast (Kutas, 1987), reading-like (Dambacher, Rolfs, Göllner, Kliegl, & Jacobs, 2009), or under the control of the reader by pushing a button (Ditman, Holcomb, & Kuperberg, 2007). Another proposal is to grant a parafoveal preview on the upcoming word during SVP without eye movements (Barber, Donamayor, & Kutas, 2010). Finally, several studies used the same sentences in separate EM and SVP experiments with different participants (Dambacher & Kliegl, 2007; Raney & Rayner, 1993; Sereno, Rayner, & Posner, 1998).

All these techniques preclude direct comparisons between EEG measures and oculomotor behavior. As a consequence, the basic relationship and temporal contingency between the dependent variables in EM research (e.g., fixation duration) and ERP research (e.g., component amplitude) is unresolved (Sereno & Rayner, 2003). On the topic of predictability, one interesting question concerns the apparent discrepancy in the timing of effects in EMs and ERPs (Sereno & Rayner, 2003; Rayner & Clifton, 2009): In normal reading, predictability acts early enough to influence the initial fixation on a word (Rayner, Binder, Ashby, & Pollatsek, 2001; Rayner et al., 2004), which lasts less than 250 ms on average. In contrast, N400 effects from SVP studies only begin to arise at 200-250 ms and reach their maximum at 400 ms or later. This raises the question whether predictability effects in both methods reflect a common underlying process, or not.

A potential alternative is to record EMs and ERPs simultaneously from the same reader. Because little or no useful information is acquired during the saccade (Matin, 1974; Ross,

Morrone, Goldberg, & Burr, 2001), fixation onsets provide natural EEG time-locking points to study information processing in normal vision. Averaged potentials aligned to fixation onsets are called fixation-related potentials (FRPs), while those aligned to saccade onsets are called saccade-related potentials (SRPs)[13].

Existing Research Integrating EM and EEG

Recording SRPs and FRPs is not a new technique. Large and single saccades, measured via electro-oculogram (EOG) electrodes near the eyes, have frequently been used in basic EEG research on post-saccadic visual processing, oculomotor preparation, and decision making (e.g., Everling, Krappmann, & Flohr, 1996; see *Methodological Discussion* for additional references). In contrast, only a handful of studies on visual word recognition have allowed for saccades. Several early studies have recorded SRPs following a single saccade towards a word presented in the periphery (e.g., Marton, Szirtes, & Breuer, 1985). Two recent studies with eye tracking (Baccino & Manunta, 2005; Simola, Holmqvist, & Lindgren, 2009) have presented pairs of words in order to investigate whether the lexicality of a parafoveal word and its semantic relation to the foveal word influence the ERP while participants still fixate the foveal word. Baccino and Manunta have reported an effect of semantic relatedness before the saccade to the parafoveal word and as early as 110 ms after stimulus onset. Simola and colleagues found a lexicality effect for parafoveal words in the right hemifield, but no evidence for parafoveal semantic access. To avoid saccade-related measuring artifacts, both studies restricted data analysis to a short segment of EEG before the first saccade.

In a study by Hutzler et al. (2007), participants read an array of five unrelated words and had to judge whether the final word had been presented as part of the array or not. The old/new effect – a late positivity for correctly recognized old words – was observed in FRPs, and also during SVP of the same words. As part of several pioneering studies on SRPs (Marton, 1991), Marton and colleagues even allowed their participants to read a full sentence from left to right (Marton & Szirtes, 1988a; 1988b). However, due to various technical constraints, the sentence-final word was displaced 20° to the left or right. After

[13] With regard to the family of visually-evoked components that follow saccade on- and offset, SRPs have also been referred to as *lambda waves* in the literature. Likewise FRPs have also been called *eye-fixation-related potentials* (EFRPs). We use SRP and FRP for averaged saccade- and fixation-aligned data, because these abbreviations are short, symmetric, and their meaning is not confined to early visual processing.

time-locking the SRP to the saccade onset, the authors observed an N400-like effect when the final word violated the sentence context. As in the study of Hutzler et al., the critical saccade was last in the sequence, so it was not possible to compare neural activity with fixation durations.

Finally, several studies have recorded SRPs during largely unconstrained scanning behavior such as reading (Barlow, 1971; Kurtzberg & Vaughan, 1979; Takeda, Sugai, & Yagi, 2001, see also Burdette, Walrath, Gross, & Stern, 1986), REM sleep (Abe, Ogawa, Nittono, & Hori, 2004), or picture viewing (Kurtzberg & Vaughan, 1979). However, without concurrent eye tracking, SRPs could not be related to fixation durations or the fixated item, but were instead aggregated across all saccades or compared globally for different stimuli or saccade types (e.g. reading vs. picture scanning, Kurtzberg & Vaughan, 1979). A study by Graupner and colleagues (Graupner, Velichkovsky, Pannasch, & Marx, 2007) allowed for free EM behavior during picture viewing. Participants scanned a scene, and distracter stimuli were occasionally flashed near current fixation. Different distracter conditions were then compared in terms of their effect on fixation duration and the visual potential evoked by distracter onset.

Methodological Challenges

To our knowledge, no study has co-registered EM and EEG in an unconstrained viewing situation in order to directly compare oculomotor behavior to brain activity as a function of the properties of the currently fixated item. This is likely due to at least four major methodological problems associated with such recordings: (1) the need to co-register precise gaze position without technical interference, (2) corneoretinal and myogenic eye movement artifacts, (3) varying degrees of overlap between brain responses elicited by successive fixations, and (4) low-level, visuomotor influences on cortical activity before and after fixation onset. In an extended *Methodological Discussion*, we review the relevant background information on each of these problems and propose solutions.

The Present Study

Given the important role of predictability in reading research, we deemed it a suitable proving ground for an attempt to co-register EMs and ERPs in saccadic vision with in- and outgoing saccades. Participants read sentences at their own pace, moving their eyes freely, with no other task than comprehension. We assumed that well-known effects could be recovered and that we may reap benefits from co-registration that go beyond what usually can be inferred from separate recordings. Data analyses are structured as follows: First, we

describe basic properties of the artifact-corrected FRP and SRP in multi-saccadic vision. Second, we demonstrate that standard word predictability effects are recovered under co-registration. Third, we establish the basic relationship between EM behavior and N400 in the same set of fixations. We will model this relation at the level of individual fixations and trace the time course of semantic processing relative to fixation onset.

Method

Participants

Thirty students (22 women, 17-37 years, mean age 23.0 years) participated in the 2.5-hour session. All were native speakers of German with a mean of 15 years of education and no history of reading difficulties or neurological/psychiatric disorders. They were paid 25 € or received course credit. All participants had normal or corrected-to-normal visual acuity (Bach, 1996). Twenty-five participants were right-handed, one left-handed, and four ambidextrous (Oldfield, 1971). Data from four additional participants was recorded but not analyzed because of EEG voltage drifts.

Apparatus

Participants were seated in a dimly lit, sound-attenuated room at a distance of 85 cm from a 17" monitor (Samsung SyncMaster 171T TFT, resolution 800 × 600 pixel, 60 Hz vertical refresh). The screen of the monitor was framed with a light grey cardboard mask that subtended 60° × 75°. The mask served to homogenize the characteristics of the visual field across different on-screen fixation locations and to reduce any resulting influences on the morphology of post-saccadic visually-evoked lambda waves (see *Methodological Discussion*).

Materials

Subjects read the *Potsdam Sentence Corpus* (Kliegl, Grabner, Rolfs, & Engbert, 2004) which contains 144 unrelated German sentences (1138 words) with a large variety of grammatical structures and semantic contents. All sentences are semantically and syntactically legal. Sentence length ranges from 5 to 11 words with a mean of 7.9 words. The corpus has previously been used to study predictability effects on EMs (Kliegl et al., 2006) and stimulus-locked ERPs (Dambacher et al., 2006). Thirty-two samples of these sentences are provided in Kliegl et al. (2004). For the present analyses, we considered only open-class words of the corpus (nouns, adjectives, verbs, adverbs; n = 813 words) and excluded words

at the beginning (word position one and two) or end (final word) of the sentence. Sentence-initial words were excluded to avoid influences of the trial-initial fixation check on fixation behavior. Sentence-final words were excluded because they tend to be fixated longer (Rayner, Kambe, & Duffy, 2000; Just & Carpenter, 1980) and elicited more positive-going ERPs (Friedman, Simson, Ritter, & Rapin, 1975; Hagoort, 2003) than words at intermediate positions ("sentence wrap-up" effects).

To study predictability effects, we used only the normal range of cloze probabilities in the sentences of the Potsdam Corpus. In order to do so, the remaining 499 words (henceforth called *target words*) were categorized according to cloze probability. The cloze probability of a word in a given sentence context is defined as the probability of correctly guessing it as the upcoming word after knowing all preceding words of the sentence. Cloze probabilities for every word in the corpus were collected in a norming study with $N = 282$ German native speakers (for details see Kliegl et al., 2004). Each participant generated predictions for a subset of the sentences, yielding 83 complete protocols for the entire corpus.

While predictability is always defined as cloze probability in the present study, it is important to note that cloze probability is typically correlated to, but not identical with, the amount of contextual constraint imposed by the preceding sentence. For example, both a weakly and a strongly constraining sentence frame can be completed by an equally unpredictable final word (e.g., Federmeier, 2007; Federmeier, Wlotko, De Ochoa-Dewald, & Kutas, 2007). We therefore also computed sentence constraint at the position of the target word, which was operationalized as the number of different predictions generated during the norming study[14]. The theoretical range of this variable was therefore from 1 (perfectly constraining sentence frame; allows only one completion) to 83 (uninformative sentence frame; every rater guesses a different upcoming word). As it is typical for a corpus of normal sentences, cloze probability correlated not only with constraint ($r = -.43$), but also with word length ($r = -.23$), word position ($r = .18$), and CELEX-based word frequency ($r = .33$; Baayen, Piepenbrock, & van Rijn, 1995). To control the influences of these covariates, they were included as predictors in a linear mixed model of N400 amplitude.

For most SRP/FRP analyses, we used a three-level categorization of *low predictable* words (cloze $p \leq .01$, $n = 187$ words), *medium predictable* words ($.01 <$ cloze $p \leq .25$, $n = 235$) and *high predictable* words (cloze $p > .25$, $n = 83$). Mean cloze probabilities for these categories

[14] The same results pattern was obtained when we defined contextual constraint not as the number of different words expected in the cloze procedure, but as the cloze probability of the most expected word.

were .00, .07, and .55, respectively (Table 3.1). To compare effects on EMs and FRPs, we also used a finer categorization into five bins, where unpredictable words (cloze $p = 0$) were assigned to the first bin and the remaining words were assigned to four additional bins each containing the same number of words.

Procedure

The experimental procedure was designed to approximate a natural reading flow, including leftwards return saccades at the end of each trial. At the beginning of the trial, a fixation point appeared on the left side of the center line of the screen (Figure 3.1A). Five-hundred milliseconds after fixation point onset, the eye tracker started to poll the participants' eye position. Once it registered a stable (> 150 ms) fixation, a full sentence was presented as one line of text on the center line of the monitor, thereby replacing the fixation point. Text was displayed in black on a white background in a monospaced font (Courier 9) at a size of 0.26° per character. The horizontal position of the sentence was set so that the initial fixation was always located slightly left of the center of the first word (the optimal viewing position, O'Regan & Lévy-Schoen, 1987). Subjects then read the sentence at their individual pace, moving the eyes freely over the words. After they finished reading, participants looked for 500 ms at a second small point near the right margin of the screen. This fixation initiated a new trial: Sentence and right fixation point disappeared and were replaced by the left fixation point, the fixation of which triggered the next sentence presentation.

The participants' task was to read the sentences and to answer simple three-alternative multiple-choice questions presented after 20% of the sentences. Questions pertained to the content of the preceding sentence and were answered by a mouse click (mean accuracy: 96%). There was no instruction to suppress eye blinks. Subjects read ten warm-up sentences before the experiment.

EM Recording

EM were recorded from the right eye with a table-mounted IView-X Hi-Speed eye tracker (SensoMotoric Instruments, Germany) at a sampling rate of 240 Hz. Viewing was binocular. The infrared video-based system has an instrument spatial resolution of < 0.025° and an absolute gaze position accuracy of up to 0.2°. Thus, calibrated eye position was recorded accurately at the level of letters. Head movements were minimized by the eye tracker's built-in chin and forehead rests. Proper calibration of the eye tracker was automatically assessed at the onset of every trial: If gaze was not detected within an invisible 0.5° × 0.5°

box around the left fixation point within 2 s, the system was recalibrated with a 13-point grid.

EEG Recording

The EEG and EOG were recorded from 32 Ag/AgCl electrodes on the scalp and around the eyes. Twenty-eight electrodes were mounted in an elastic electrode cap (Easycap GmbH, Germany) at positions FP1, FP2, Fz, F3, F4, F7, F8, FC5, FC6, FT9, FT10, Cz, C3, C4, T7, T8, A2, CP5, CP6, Pz, P3, P4, P7, P8, PO9, PO10, O1, and O2 of the International 10/10 system. Four EOG electrodes were affixed to the outer canthi and infraorbital ridges of both eyes. Foam-cushions were fitted to the participants' forehead to preclude pressure artifacts from contact between frontal electrodes and the eye tracker's forehead rest. Seating position and head position in the eye tracker were carefully adapted to avoid myogenic interspersion from neck and temple muscles. Impedances were kept below 5 kΩ. An additional electrode at FPz served as ground. Signals were amplified with a Brainamp AC amplifier (Brain Products GmbH, Germany) at a band-pass of 0.01 - 70 Hz and digitized at a rate of 250 Hz. All electrodes were initially referenced to left mastoid (A1), but converted to average reference offline, thereby recovering A1 as a recording electrode. Thus, the data of 33 electrodes entered the analyses. For use in artifact correction, 3D electrode locations were determined with a Zebris CMS20 digitizer (Zebris Medical GmbH, Germany). To synchronize EM and EEG records, a common TTL trigger was sent at the beginning and end of each trial from the stimulus presentation PC (running *Presentation* Software, Neurobehavioral Systems Inc, Albany, CA) and looped through to two additional PCs recording EMs and EEG.

EM Analysis

The EM record was screened for loss of measurement and eye blinks. If a sentence contained only a single blink very early (<200 ms) or late (>2 s) after sentence onset (12.8 % of trials), the remaining data was used for fixation detection. Otherwise, or if multiple blinks occurred, the trial was discarded (5.1 % of trials). Saccades were detected as outliers in two-dimensional-velocity space with the monocular variant of the algorithm detailed in Engbert and Mergenthaler (2006). Saccade detection led to a total pool of 38,538 reading fixations. In a first level of screening, we discarded 2,775 fixations that occurred during intervals in which the EEG contained non-ocular artifacts. In a second step, the pool was constrained to 22,321 fixations that occurred more than 700 ms after sentence onset. Earlier fixations were excluded to avoid temporal overlap between FRPs and the ERP

evoked by the screen onset of the sentence. In line with previous experiments with the Potsdam Corpus (Kliegl et al., 2006), we eliminated extremely short (<50 ms, *n* = 1,157) or long (>750 ms, *n* = 64) fixations. In a final step, the pool was restricted to *first* fixations on *target words* in *first-pass reading*: 12,607 of the remaining fixations were on targets, 9,237 fixations of these were first fixations rather than refixations, and 7,113 occurred in first-pass reading. All EM and EEG analyses were based on this final pool of 7,113 fixations. Because fixations with a bad concurrent EEG record were removed, EM and FRP analyses were always conducted on the exact same set of fixations.

Dependent variables for behavioral analyses were first-fixation duration (FFD) and gaze duration (GD). Gaze duration is defined as FFD plus the duration of all immediate refixations. FFD and GD were submitted to repeated-measures analyses of variance (ANOVAs) on the factor predictability. Results are reported with *p* values corrected for violations of sphericity according to Huynh & Feldt (1976), the original degrees of freedom, and the epsilon (ε) value.

EEG Ocular Artifact Correction

To correct for corneoretinal eye movement artifacts (see *Methodological Discussion*), we applied Surrogate Multiple Source Eye Correction (MSEC; Berg & Scherg, 1994; Ille, Berg, & Scherg, 2002) as implemented in BESA (v. 5.1; MEGIS Software GmbH, Germany). The method combines the recording of calibration eye movements, Principal Component Analysis (PCA), and dipole modeling to separate artifact and brain activity. In surrogate MSEC, characteristic scalp topographies for different types of ocular artifacts are derived for each participant by averaging calibration eye movements. In addition to these empirically derived artifact topographies, a set of brain signal topographies is defined by a generic dipole model of the brain, which is identical for all participants. Importantly, this "surrogate" brain model is not used to directly model the artifact-free EEG, but its purpose is to preclude the subtraction of genuine brain activity that is spatially correlated to the artifact. Based on these spatial definitions for artifact and brain activity, a linear inverse operator is computed that decomposes the experimental data into linear combinations of brain and artifact activity, that is, the activation time courses for the artifact topographies are determined in the presence of the brain model. In a final step, this estimated artifact activity is subtracted from the raw EEG.

Technical details were as follows: In a 15-minute session before the experiment, participants performed 120 calibration saccades (15° amplitude) in the four cardinal

directions. Saccades were aimed at targets on the mask surrounding the monitor. Saccade direction was indicated by an arrow, which appeared in the screen center every three seconds. In addition, 40 spontaneous eye blinks were recorded during fixation. Short EEG segments following each of the three movement types (vertical, horizontal, blink) were then averaged and subjected to three separate PCAs. The first PCA factor (typically explaining > 97% variance) was used to define the topography for each type of artifact. Note that PCA was used here as an optional preprocessing step (see Berg & Scherg, 1994) to extract the most characteristic artifact topographies from calibration data; PCA was not applied to the experimental data. Brain signal topographies were defined by BESA model *RS4.par.* This model contains 12 dipoles with fixed location and orientation, placed at spatially distributed, strategic positions of the brain. After defining artifact and brain topographies, the activity time course for each topography was determined in the experimental data using the spatial filter operator detailed in Ille et al. (2002, p. 123). For correction, the activity assigned to the artifact topographies was subtracted. After MSEC, the corrected continuous data were high pass-filtered at 0.25 Hz (48 dB/octave) and EOG channels were treated as regular EEG channels. Application of surrogate MSEC is detailed in Scherg (2003). Recommendations for recording clean calibration movements are given by Ruchkin (in Berg, 2002, p. 7-2). A comparison with other correction methods is provided by Ille et al. (2002).

Fixation-locked EEG

Around each fixation, a 1600 ms segment of EEG was cut (from 600 ms before to 1000 ms after fixation onset) and baseline-corrected by subtracting the mean voltage in the 100 ms interval prior to fixation onset. To reject muscle or drift artifacts, we discarded segments with absolute voltages in any channel > 100 µV or with a peak-to-peak voltage difference > 150 µV. Joint EM and EEG analyses were performed in MATLAB (The Mathworks Inc., USA) using selected functions of the EEGLAB toolbox (Delorme & Makeig, 2004).

Evaluation of ocular correction

The synchronized eye tracking data served as a new criterion to assess ocular correction quality. For this purpose, a corresponding set of fixation-locked segments was also cut from the original, uncorrected EEG. For each corrected and uncorrected segment, the correlation between each EEG channel (downsampled to 240 Hz) and the horizontal component of the eye track was computed in an interval from -100 to 1000 ms around fixation onset. Correlation coefficients for individual segments were Fisher's *z* transformed, averaged

within each participant and then across participants. Correlations before and after ocular correction were tested against zero for each channel with a paired *t*-test.

Analysis of predictability effects

Artifact-corrected segments were averaged according to the predictability of the fixated word. To test for the presence of an N400 effect, mean amplitude in the traditional N400 window (300-500 ms after fixation onset) was submitted to a repeated-measures ANOVA on the factors *predictability* and *electrode*. To estimate a discrete time point for the onset and peak of the N400 effect, we used the difference wave between the two extreme predictability conditions (low minus high predictable) at electrode Pz, low-pass filtered at 10 Hz (zero-phase). N400 onset was determined with consecutive, sample-by-sample *t*-tests on this difference wave between -300 and 600 ms around fixation onset. The *t-max* permutation test of Blair and Karniski (1993) was used to control for multiple testing.[15]

N400 peak latency was defined as the time of the maximum absolute voltage in the grand average difference wave between 0 - 800 ms. To test for a lateralization of N400 effects, effect amplitude (low minus high predictable words, 300-500 ms) was aggregated over all 15 left- and all 15 right-hemisphere electrodes and compared with a *t*-test, leaving out the three midline sites.

Analysis of EM-EEG relationship

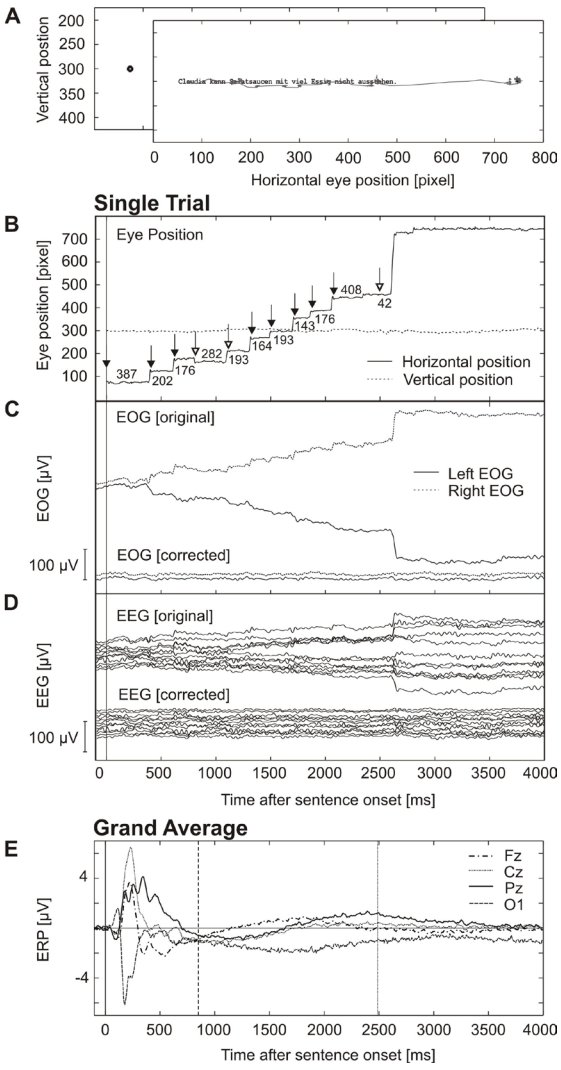
To explore the relative timing of EM and EEG measures, we analyzed on which word participants were fixating at the onset and peak of the N400 effect. For the same purpose, we also computed an additional average, aligned to the saccade that terminated the first fixation on the target. In analogy to response-locked averages in traditional ERPs, this SRP reveals whether or not, on average, N400 effects arise prior to the initiation of the next saccade, that is, during the initial fixation on the word. For this analysis, the baseline remained identical, that is, SRP segments were baseline-corrected with the baseline still placed before the onset of the preceding target fixation. An analogous *t-max* statistic was computed also for this average.

[15] During 10,000 data permutations, the sign of each single-subject difference wave was randomly assigned, *t*-values were again computed for every sampling point, and the *t*-value with the maximum absolute value was stored. This resulted in a distribution of 10,000 maximum *t*-values expected under the null hypothesis, i.e., with randomly shuffled conditions. N400 onset was defined as the first sample of the recorded waveform where the *t*-value was below (more negative than) the 5th percentile of the *t-max* distribution (t = -3.33 for the FRP). This tested the directed hypothesis of more negative voltages for low predictable words.

To test for a between-subject linear relation between predictability effects in EM and N400 amplitude, the size of the predictability effect on behavior (FFD and GD) was correlated with that on the FRP *across* participants. For this analysis, target words were categorized as low or high predictable via a split at the median cloze probability of 0.024.

Of special concern was the relation between fixation duration and N400 amplitude at the level of individual fixations. We specified linear mixed models, with the N400 amplitude following each individual fixation as dependent variable, and word and sentence characteristics (predictability, frequency, length, constraint, word position) as well as either the log of FFD or the log of GD as linear covariates (fixed effects). Predictability values were logit-transformed (logit *cloze p* = 0.5 * ln(*cloze p*/(1-*cloze p*)); see Kliegl et al., 2006) before they entered the model (and also for Figure 3.5A). Participants and words were included as crossed random factors. For parameter estimation we used the *lmer* program of the *lme4* package (Bates & Maechler, 2009) in the R system for statistical computing (R Development Core Team, 2009). These regression analyses model the variance of the N400 differences between participants and between words on the assumption that they are normally distributed.

Figure 3.1



A. Trial scheme and data for a typical sentence. Each trial began with a fixation point on the left. Once the eye tracker detected a precise fixation, a single sentence was displayed as one line of text. Participants read the sentence at their individual pace, moving the eyes freely over the text. Eye movements are plotted for one subject reading the sentence "*Claudia kann Salatsaucen mit viel Essig nicht ausstehen*." (Claudia cannot stand salad dressings with lots of vinegar.). After reading the sentence, participants looked at a point on the right. Gaze-controlled presentation ensured a continuous reading flow including leftwards return saccades to read a new sentence. **B.** Horizontal and vertical gaze position. The sentence appeared at time 0. Solid arrows indicate the onsets of first fixations, open arrows mark refixations. Fixation durations are given in milliseconds. **C.** Signal at left and right horizontal EOG electrode before and after corneoretinal artifact correction. **D.** Synchronized EEG record for a subset of channels before and after correction. **E.** Grand average artifact-corrected ERP, time-locked to sentence onset. The dotted line indicates mean sentence-reading duration. To avoid overlap between potentials evoked by sentence onset and those evoked by individual reading fixations, only fixations were considered that occurred >700 ms after sentence onset (dashed line).

Table 3.1. Target word properties and resulting effects on EM behavior and FRP amplitude

		Predictability				
	All targets	Low	Medium	High	*F*	*p*
A. Word and sentence properties						
Cloze probability	0.12 (0.21)	0.01 (0.00)	0.07 (0.07)	0.54 (0.21)	977.4	.000
Word length (char.)	5.8 (2.7)	6.6 (2.7)	5.4 (2.5)	4.9 (2.3)	17.2	.000
CELEX frequency (log, per million)	4.7 (1.3)	4.0 (1.2)	5.1 (1.2)	5.3 (1.2)	50.8	.000
Word position in sentence	5.0 (1.7)	4.6 (1.6)	5.1 (1.7)	5.8 (1.6)	14.8	.000
Sent. constraint (N guessed words)	25.1 (11.0)	27.8 (10.8)	26.3 (10.7)	15.4 (6.3)	45.6	.000
Sentence length (words)	8.2 (1.4)	8.2 (1.5)	8.2 (1.3)	8.4 (1.3)	0.6	n.s.
B. EM behavior						
FFD (ms)	224 (25)	235 (28)	219 (25)	213 (21)	39.2	.000
GD (ms)	278 (41)	304 (54)	268 (38)	247 (34)	57.5	.000
Refixation probability	0.24 (0.07)	0.28 (0.10)	0.22 (0.08)	0.18 (0.09)	24.9	.000
Duration prev. fixation n-1 (ms)	213 (25)	214 (26)	210 (24)	217 (29)	3.5	.046
Duration next fixation n+1 (ms)	212 (32)	216 (29)	210 (34)	207 (38)	4.0	.025
Incoming saccade amplitude (°)	2.0 (0.5)	2.0 (0.5)	1.9 (0.5)	2.0 (0.5)	3.5	.037
Outgoing saccade amplitude (°)	1.4 (0.6)	1.4 (0.6)	1.4 (0.6)	1.5 (0.7)	1.2	n.s.
Fixated after sentence onset (ms)	1301 (198)	1244 (177)	1300 (208)	1431 (253)	63.9	.000
Sentence reading duration (ms)	2490 (713)	2566 (737)	2465 (704)	2400 (687)	29.1	.000
C. FRP						
Amplitude at Pz, 300-500 ms (μV)	-0.77 (0.62)	-1.27 (0.90)	-0.69 (0.74)	0.03 (1.31)	15.8	.000

Note. Given are means and standard deviations. Statistics are based on words in **A**. and on fixations in **B**. & **C**.

Results

Results are organized in six sections. First, we present standard EM effects that establish the ecological validity of the data. Second, we report measures for the quality of ocular artifact correction. Passing these checks was a precondition for the validity of FRP results. Third, we describe the FRP over the course of reading an entire sentence. In particular, sentence onset evoked a potential that spilled over to different degrees in the FRPs, forcing the exclusion of some fixations from the following analyses. Fourth, we introduce the artifact-corrected FRP as an EEG measure. Since FRPs have not been described in detail for natural viewing situations, we describe how pre-saccadic motor potentials, post-saccadic visual potentials, and overlapping potentials influence the results. Fifth, we present word predictability effects on FRPs. Finally, we compare EM and EEG effects and map them onto a common timeline.

Eye Movements

Eye movements for a typical trial are shown in Figure 3.1. On average, participants read the sentence for 2490 ms (*SE* = 130 ms) before they initiated the final saccade towards the right fixation point. Mean FFD on target words was 224 ms (*SE* = 5 ms). Targets received at least one refixation in 24% of the cases, resulting in a mean gaze duration of 278 ms (*SE* = 8 ms).

Word predictability clearly influenced EM behavior[16]. On average, low predictable words were fixated 22 ms longer than high predictable words upon first fixation (low: 235 ms, medium: 219 ms, high: 213 ms, $F(2,58) = 39.2$, $p < .001$, $\varepsilon = .90$, $\eta_p^2 = .58$). Gaze duration was 57 ms longer for low predictable than high predictable words (low: 304, medium: 268, high: 247; $F(2,58) = 57.5$, $p < .001$, $\varepsilon = .87$, $\eta_p^2 = .67$). Due to these effects, total sentence reading duration also differed between predictability levels, $F(2,58) = 29.1$, $p < .001$, $\varepsilon = .96$, $\eta_p^2 = .50$ (Table 3.1).

Of special methodological importance were differences in the amplitude of the incoming and outgoing saccade. This is because saccade amplitude per se influences the morphology of saccade-related visuomotor brain potentials, independent of the distortion by eye movement artifacts (see *Methodological Discussion*). Importantly, outgoing saccade amplitude did not differ as a function of word predictability. Incoming saccade amplitude was slightly smaller for fixations on medium-predictable words (low: 2.0°, medium: 1.9°, high: 2.0°; $F(2,58) = 3.5$, $p < .05$, $\varepsilon = .95$, $\eta^2 = .27$, see Table 3.1) but we will show later on that this difference of less than 0.1° is unlikely to have a relevant impact on the FRP.

[16] To ensure that predictability accounted for variance in EM measures under concurrent control of other word and sentence properties, we specified two control models with either FFD or GD as dependent variable, and the six variables from Model 2 (*pred*, *freq*, *pred × freq*, *length*, *constraint*, and *word position*, see Table 3.3) as predictors. Predictability was a significant predictor of both FFD (*t*-value = -4.5) and GD (*t* = -6.0). Other significant predictors of FFD were *constraint* (-3.7), and the *pred* × *freq* (2.8) interaction. Other significant predictors for GD were *word length* (13.6), *word position* (3.2), and *pred* × *freq* (4.7).

Table 3.2. Correlation between EEG & horizontal eye track

Hemisphere	Electrode	Original	Corrected
Midline	Fz	.07	.05
	Cz	-.02	.02
	Pz	.01	.03
Left	hEOG	-.97	-.04
	T7	-.63	-.05
	C3	-.32	.00
	P3	-.17	.00
	O1	-.06	.01
Right	hEOG	.97	-.02
	T8	.57	.00
	C4	.24	.01
	P4	.14	.03
	O2	.07	.04

Note. Shown are mean correlations for selected electrodes before and after MSEC. hEOG = horizontal EOG electrode. Correlations that differ significantly from zero are printed in bold.

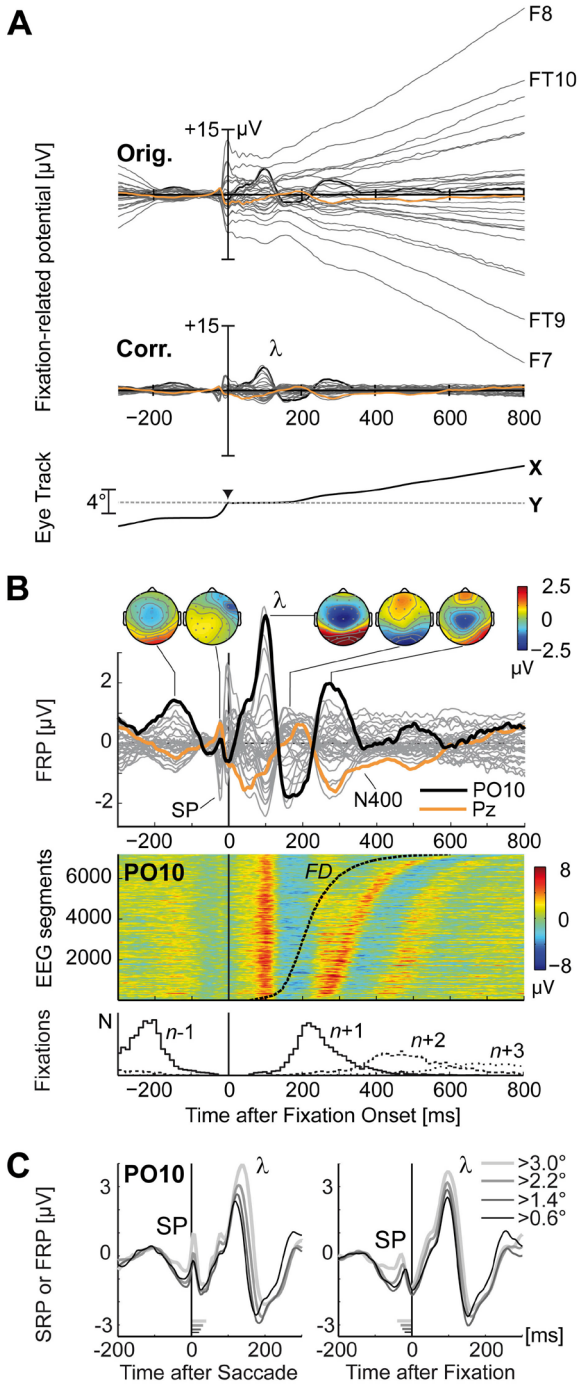
Quality of Artifact Correction

EEG correction quality was assessed with three criteria: (1) Visual impression of the continuous EEG, (2) voltage differences between left- and right-hemisphere electrodes in the averaged FRP, and (3) residual correlations between gaze position and EEG after MSEC correction. Figure 3.1 provides an example of the continuous EOG (Figure 3.1C) and EEG (Figure 3.1D) before and after correction. After correction, it was generally not possible to visually identify residual artifacts in the continuous data. Figure 3.2A shows the FRP, superimposed for all channels, before and after correction. Before correction, large distortions from the predominantly rightward-going saccades were evident, with positive distortions at right-hemisphere electrodes and negative distortions at left-hemisphere electrodes. As the incoming saccade was usually followed by more right-going saccades, artifacts from multiple saccades summed up towards the end of the segment. At +1000 ms, temporal electrodes T7 and T8 differed in voltage by about 100 μV.

After correction, signals at all channels were in the typical ERP amplitude range (Figure 3.2A). Although artifacts were drastically reduced, some fronto-lateral channels still showed indications of reversed polarities on opposite sides of the head towards the very end of the segment. This suggests that correction across several saccades was not perfect for these electrodes. As a new quantitative measure, we computed linear correlations between each EEG channel and the horizontal component of the eye track. Before correction, 31 of 33 channels correlated significantly ($|t(29)| > 2.05$, $p < .05$) with gaze position, with maximum correlations at electrodes near the eyes (see Table 3.2). The horizontal EOG electrodes each showed a near-perfect correlation with gaze position ($r = \pm.97$), which increased to $r = .99$ in a bipolar EOG montage (right minus left). After MSEC, correlations at all channels were close to zero (max. $|r| = .07$; max. $R^2 = .005$), suggesting that the residual variance accounted for by horizontal saccades was small. Nevertheless, correlations remained significantly different from zero for about half (18 of 33) of the channels. Electrodes on the posterior sagittal midline were least affected by horizontal saccades, but Cz and Pz were the only two electrodes not significantly correlated with gaze, even in the uncorrected data. Because Pz contained little or no corneoretinal artifact in the first place, effects of correction were minimal at this electrode.

While MSEC removed most of the corneoretinal artifact, it only partially removed the brief muscle spike potential (Keren, Yuval-Greenberg, & Deouell, 2010) at saccade onset. Nevertheless, MSEC attenuated the spike potential because its topography overlaps with that of corneoretinal artifacts (see also Methodological Discussion).

Figure 3.2



OCULAR ARTIFACTS

OVERLAP

LOW-LEVEL

The fixation-related potential in multi-saccadic vision. **A**. Grand average FRP for 7,113 target fixations before and after corneoretinal artifact correction. Time 0 marks fixation onset. Signals at all EEG electrodes are shown superimposed. Prior to MSEC (Orig.), frontal and temporal channels were strongly distorted. After MSEC (Corr.), artifacts are largely eliminated and genuine brain activity becomes visible. Midline electrode Pz (orange line) was unaffected by corneoretinal artifacts, even before correction. **B**. Top. Properties of the grand average FRP. Maps depict scalp topographies at five component peaks: (1) the visually-evoked lambda response evoked by previous fixation n-1, (2) the myogenic spike potential (SP) at saccade onset, (3) the lambda response evoked by current fixation n, which peaked after 104 ms at parieto-occipital electrodes PO9 and PO10, (4) the equivalent of the N170 component, and finally (5) the N400 component, overlapped by the lambda response from fixation n+1. Middle. Each horizontal line in the ERPimage represents one of the 7,113 EEG segments that entered the average shown above. Amplitude is coded as color. Segments were sorted by first fixation duration and then smoothed vertically with a moving average across 50 adjacent segments. Sorting shows how the second positive peak at around 280 ms is partially explained by the lambda response from fixation n+1. Because contributions from successive fixations are increasingly time-jittered, the overall waveshape of the FRP resembles a damped oscillation. Bottom. Histogram of onset latencies of preceding and subsequent fixations. **C**. Effect of saccade size on the morphology of SRPs and FRPs. The amplitude of the spike potential and the lambda response increased with saccade size.

Sentence-onset ERP

Figure 3.1E shows the artifact-corrected ERP time-locked to the screen onset of the sentence. Sentence onset elicited a large ERP, whose dominant component was a temporally extended P300 with a characteristic centroparietal-positive scalp distribution. To avoid a carry-over of this stimulus-evoked ERP into the fixation-locked segments, only fixations were analyzed that occurred > 700 ms after sentence onset, when this ERP had returned to baseline. Still, on average, the remaining low predictable words occurred at earlier sentence positions and were fixated sooner after sentence onset than high predictable words (see Table 3.1). To ensure that the EEG background activity was not different at the time the target was fixated, we calculated the mean amplitude in the 100 ms pre-*fixation* baseline relative to a 100 ms pre-*stimulus* baseline before sentence onset. An analysis of variance of these "absolute" pre-fixation baseline amplitudes as dependent variable, and predictability level and electrode as factors, yielded a non-significant result, $F(64,1856) < 1$. This suggests that FRPs occurred against a similar baseline in all predictability conditions.

Figure 3.1E shows that between 700 ms and the mean reading duration of 2490 ms, the sentence-locked ERP was characterized by a slow positive shift at frontal and central electrodes and a relative negativity at occipital sites. This sentence-level ERP during normal reading has not been described before and may be theoretically interesting as a phenomenon on its own. However, the present data does not allow us to distinguish whether these late ERP fluctuations reflect sentence-level processing demands (e.g., working memory load) or merely the superposition of many individual FRPs over the course of reading.

Fixation-Related Potentials in Natural Vision

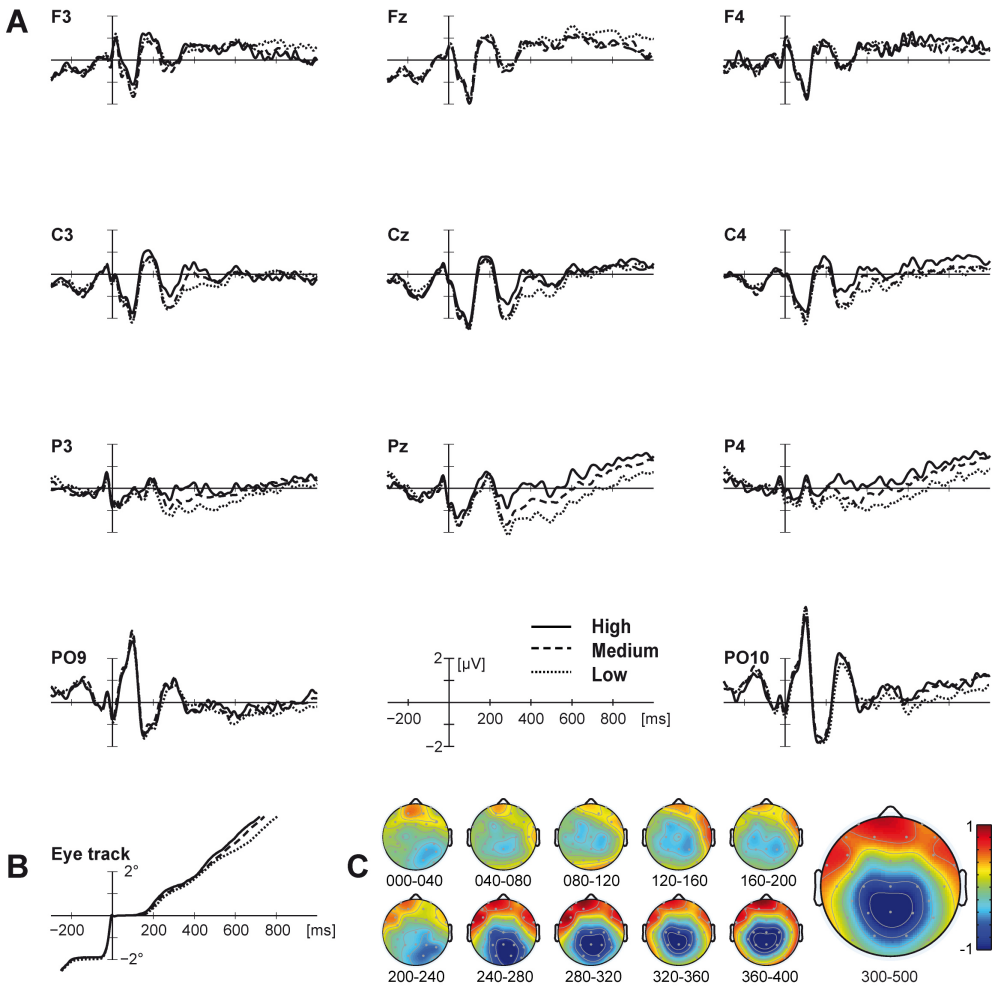
Figure 3.2 summarizes the features of the FRP after artifact correction. The *post*-fixation waveshape was dominated by the visually-evoked lambda response (Kazai & Yagi, 2003), which peaked after 104 ms (SE = 1.3 ms). It was largest at lateral-occipital electrode PO10 over right visual cortex (amplitude: M = 4.4 µV, SE = 0.3 µV), but also influenced the waveshape at frontal electrodes with a reversed polarity (cf. also Figure 3.3A). The lambda response is considered primarily a visual response (Riemslag, van der Heijde, & van Dongen, 1987; Thickbroom, Knezevic, Carroll, & Mastaglia, 1991) which is most likely generated in striate or early extrastriate cortex (Kazai & Yagi, 2003; Dimigen, Valsecchi, Sommer, & Kliegl, 2009). Because the average interval between any two reading fixations

was only 233 ms, the waveshape of the FRP was characterized by overlapping lambda responses from preceding and subsequent fixations. As shown in Figure 3.2B, a second occipital peak after 280 ms reflected the summation of a potential evoked by the current fixation *n* and the lambda response elicited by fixation *n*+1. Due to normal variance in fixation duration, overlapping contributions from adjacent fixations are time-jittered. The FRP in natural vision therefore resembles a damped oscillation with an increasingly jittered occipital peak about every 250 ms.

The *pre*-fixation waveshape was influenced by correlates of oculomotor preparation and execution, in particular the pre-saccadic spike potential. The spike potential is a sharp, biphasic spike at saccade onset that is believed to reflect summated electric activity of the oculomotor nerves or muscles. It is best seen in SRPs (cf. Figures 3.2C and 3.4A), and smeared in FRPs due to variance in saccade duration. The spike potential showed the typical topography, which is reversed relative to the corneoretinal artifact: a frontal negativity, shifted ipsilateral to saccade direction, and a parietal positivity, shifted contralateral to saccade direction. For large reading saccades (> 3°), there was also some indication of an earlier posterior positivity that culminated into the spike potential (Figure 3.2C, right panel). This may be the *pre-saccadic positivity* (also called antecedent potential) a slow, ramp-like potential found prior to voluntary saccades and believed to reflect saccade preparation in cortical structures (Everling et al., 1996; Richards, 2003).

Figure 3.2C compares FRPs and SRPs for different saccade sizes. Both the spike potential and the visual lambda response increased with increasing saccade size (see also *Methodological Discussion*).

Figure 3.3



Predictability effect in FRPs. **A**. The grand average FRP, time-locked to first fixation on the target word (time 0) shows a graded effect of word predictability that is largest at centroparietal electrode Pz. **B**. Mean horizontal component of the eye track. **C**. Scalp distributions of the predictability effect (low minus high) are shown for successive 40 ms windows after fixation onset and for the traditional N400 window (300-500 ms).

Predictability Effects in FRPs

Figure 3.3A shows that predictability clearly modulated the FRP evoked after the initial fixation on the word: Words with little contextual support elicited more negative voltages at centroparietal scalp sites. The presence of an N400 effect was confirmed by a *Predictability* × *Electrode* interaction, $F(64, 1856) = 4.84$, $p < .001$, $\varepsilon = .13$, $\eta_p 2 = .14$, in the 300-500 ms time window (effects across the whole scalp are only meaningful in interaction with electrode, because the average reference sets the mean of all electrodes to zero). Pairwise comparisons between predictability levels showed that the interaction with

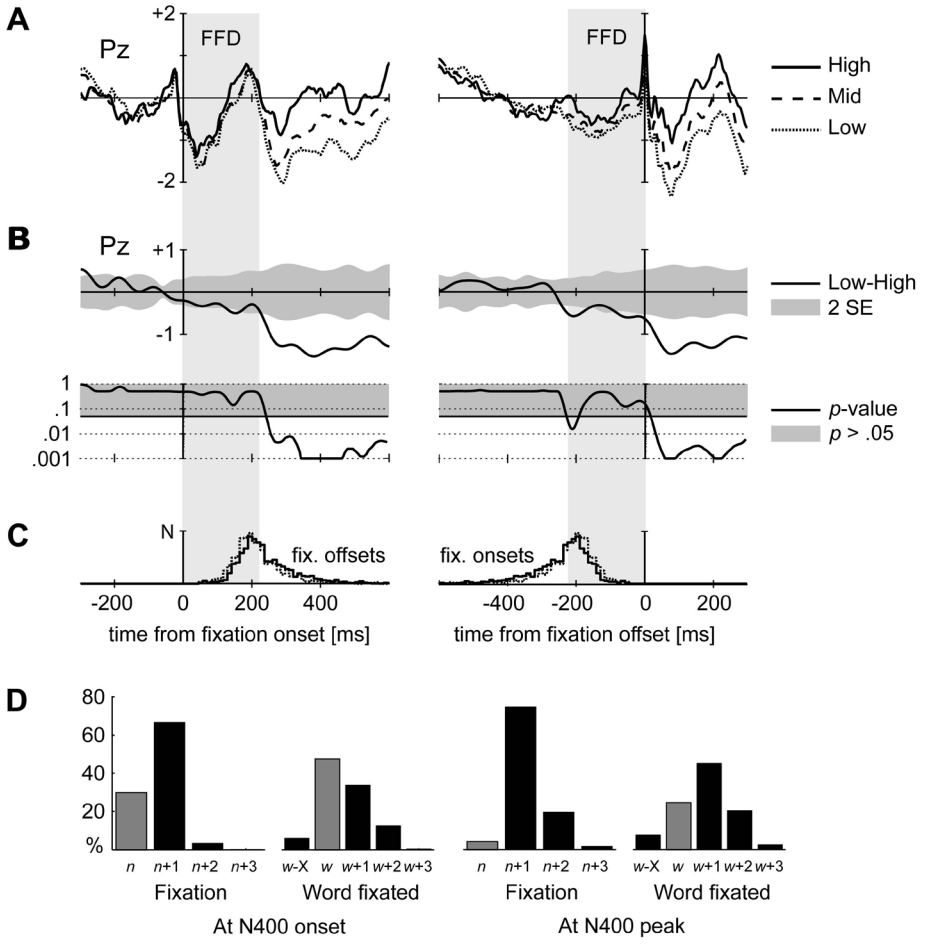
electrode was significant for the contrast *low* vs. *high, F*(32,928) = 4.82, $p < .001$, marginally significant for *low* vs. *medium* ($p = .07$), and not significant ($p = .19$) for *medium* vs. *high* predictable words. All three comparisons were significant (at $p < 0.01$) when the main effect of predictability was tested only at electrode Pz.

Importantly, the centroparietal distribution of the N400 with a maximum over Pz (Figure 3.3C) resembled that observed in many SVP experiments (Kutas, Van Petten, & Kluender, 2006). However, while effects in SVP studies are often shifted slightly towards the right hemisphere, no evidence for lateralization was found in normal reading; effect amplitude did not differ between the left and the right hemisphere ($p = .49$).

For comparison with fixation durations, a discrete time point for the onset and peak of the N400 effect was determined in the difference wave at Pz (see Figure 3.4B). At Pz, a sustained N400 effect began 248 ms after fixation onset and peaked 384 ms after fixation onset with an effect amplitude of 1.53 μV. Interestingly, much weaker N400-like central negativities, qualitatively resembling the topography between 300-500 ms, could also be seen in earlier intervals (in particular between about 120-160 ms, see Figure 3.3C), but did not survive correction for multiple comparisons. Nevertheless, they indicate that the semantic processing underlying the N400 may begin earlier - possibly only on a subset of fixations - than suggested by our strict onset criterion. No predictability effects were observed prior to the onset of the first fixation (i.e., there was no parafovea-on-fovea effect). This was also the case when the baseline interval was moved further away from fixation onset.

Finally, N400 onset was also determined relative to the *offset* of the first fixation by time-locking backward to the following saccade (SRP). In this analysis, a sustained N400 effect began 20 ms after the end of the first fixation. Additionally, an only temporary significant effect was observed in an early interval from -228 to -192 ms before fixation offset.

Figure 3.4



Relative timing of predictability effects. **A.** Grand mean FRP at Pz aligned to the onset (FRP, left side) and offset (SRP, right side) of the first fixation on the word. Grey boxes indicate mean FFD. **B.** *Upper panel*: Difference wave between low and high predictable words, which shows the effect of word predictability devoid of common overlapping activities. Shading indicates the 95% confidence interval without correction for multiple testing. *Lower panel*: corresponding p-values from the permutation test. Significant effects ($p < .05$) are indicated by points outside the grey shaded area. In the FRP, an effect of word predictability was observed starting 248 ms after fixation onset, which peaked at 384 ms in the grand average. **C.** Distribution of fixation offset and onset latencies relative to the time-locking point. **D.** Gaze position at onset (248 ms) and peak (384 ms) of the N400 predictability effect. w-X: The reader regressed to an earlier word in the sentence.

EM-EEG relationship

A unique feature of the dataset was the possibility of comparing FRP effects to corresponding modulations in EM behavior. Four analyses explored this relationship: First,

we investigated at what time FRP effects arose relative to those on behavior. Figure 3.4 shows the predictability effect at Pz, relative to the beginning and end of the first fixation. When the N400 effect peaked in FRPs (384 ms), readers had already terminated the initial fixation on the target word (fixation *n*) in 96% of the cases. Instead, as Figure 3.4D shows, readers were typically already engaged in fixation *n*+1 (75%) or *n*+2 (19%; saccade intervals were assigned to the following fixation in this analysis). On the level of words, we found that in only 25% of the cases, readers were still looking at the target (word *w*) at the latency of the N400 peak. These were mostly cases where the word was refixated. Instead, readers had typically moved on to the next words *w*+1 (45%) or *w*+2 (20%). A somewhat different picture emerged when N400 onset latency was considered: In 30% of the cases, the statistical onset latency of the N400 effect (248 ms) fell into the first fixation on the word. In many more cases (67%), it fell only into the following fixation *n*+1. However, because fixation *n*+1 was sometimes a refixation (in 24% of the cases), readers were still looking at the target word in about half (47%) of the cases at the statistical N400 onset latency.

Second, we compared EM and FRP effects over five levels of predictability. As Figure 3.5A shows, both N400 amplitude and GD (as well as refixation probability, which is one aspect of GD) were monotonic functions of predictability. Only for FFD was there a discontinuity in the higher predictability range. While N400 amplitude was an approximately linear function of logit-scaled predictability, Figure 3.5A indicates that behavioral measures, in particular FFD, differentiated better in the low than in the high predictability range.

Third, we investigated whether participants with large predictability effects in FRPs also exhibit large behavioral effects. Figure 3.5b shows that of 30 participants, 25 showed a predictability effect in the expected direction in both measures, supporting the reliability of the co-registration data. However, when these difference scores were correlated across *participants*, N400 amplitude correlated neither with FFD (r = -.07, p = .70) nor GD (r = .15, p = .42).

Fourth, in separate linear mixed models, we regressed FRP amplitude after each individual fixation in the N400 time window on the two EM measures, FFD and GD, respectively. Gaze duration was found to be a strong and significant (i.e., $|t|>2$) predictor of N400 amplitude (b = -0.62, SE = 0.17, t = -3.71) whereas FFD showed only a numerical trend in the expected direction (b = -0.37, SE = 0.21, t = -1.73; see Model 1 in Table 3.3). In a second step, we included lexical and sentential properties into the model. Both N400 amplitude and the EM measures are known to relate to the (logit of) word predictability and the (logarithm of) word frequency of the fixated words, as well as to the interaction between both variables

(Dambacher et al., 2006). Predictability, frequency, and their multiplicative interaction were therefore included as predictors in the model. Additionally, we included the covariates word length, contextual constraint, and word position.

Results are shown in Table 3.3 (Model 2). Of the newly included predictors, predictability, frequency, word position, and the predictability × frequency interaction were highly significant, while constraint and length had no effect on N400. Predictability was therefore a significant predictor of N400 amplitude under statistical control of other variables correlated with predictability in the sentence material. Importantly, gaze duration remained a significant predictor in Model 2. Thus, there is shared variance between GD and N400 amplitude that is not covered by the word or sentence properties included in our model.[17]

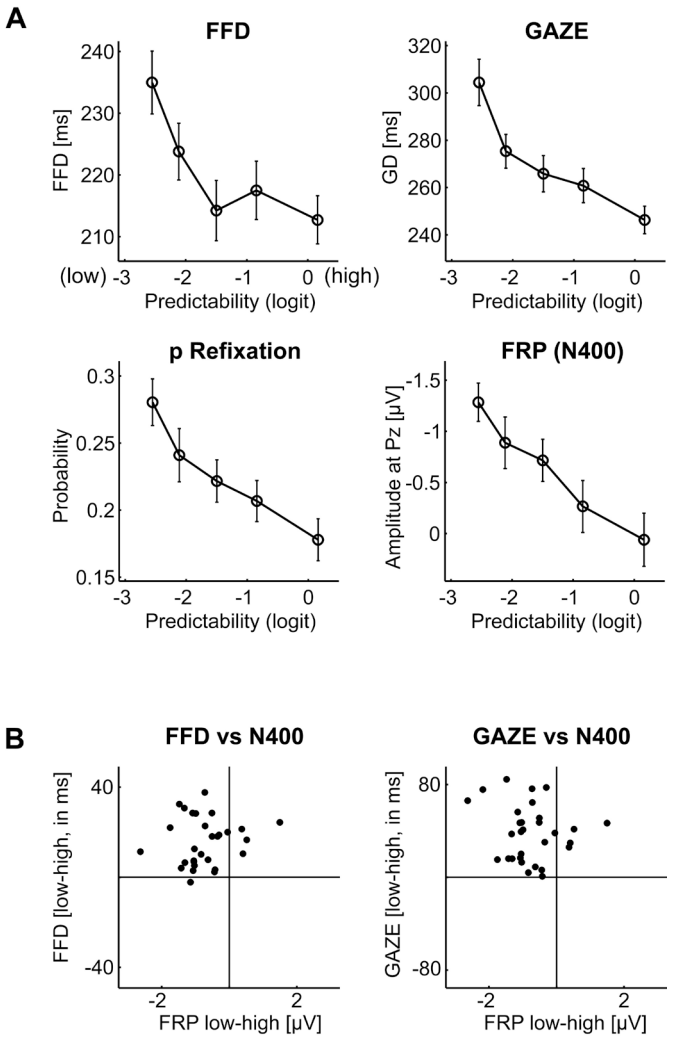
Table 3.3. Regressions of N400 amplitude on EM behavior and word/sentence properties

	FFD as predictor				*GD as predictor*			
		b	*SE*	*t*		*b*	*SE*	*t*
Model 1	Intercept	1.12	1.15	0.98	Intercept	2.63	0.94	2.81
	log(*FFD*)	-0.37	0.21	-1.73	log(*GD*)	-0.62	0.17	-3.71
Model 2	Intercept	3.03	1.30	2.34	Intercept	4.95	1.20	4.11
	log(*FFD*)	-0.31	0.21	-1.47	log(*GD*)	-0.67	0.18	-3.71
	pred	1.00	0.30	3.34	*pred*	0.91	0.33	2.73
	freq	-0.35	0.13	-2.77	*freq*	-0.34	0.14	-2.42
	length	0.02	0.03	0.69	*length*	0.05	0.04	1.38
	constraint	-0.01	0.01	-1.63	*constraint*	-0.01	0.01	-1.59
	pos	0.29	0.05	6.09	*pos*	0.30	0.05	5.72
	pred×freq	-0.15	0.06	-2.48	*pred×freq*	-0.13	0.07	-2.05

Note. Dependent variable is always N400 amplitude (mean amplitude 300-500 ms at Pz). Predictors: first fixation duration (*FFD*), gaze duration (*GD*), logit of predictability (*pred*), log of frequency (*freq*), word length (*length*), number of words predicted (*constraint*), word position (*pos*), interaction of pred and freq (*pred×freq*). *N* of observations: 7,113; *N* of subjects: 30, *N* of unique words: 499.

[17] The same inferences resulted from likelihood-ratio tests of these models. Adding sentence- and word-properties as predictors significantly improved the model fit both with FFD, Chi-square(6) = 58.0, $p < .0001$, and with GD as first predictor in the model, Chi-square(6) = 101.1, $p < .0001$. Conversely, dropping FFD from the model did not significantly decrease the fit, Chi-square(1) = 2.1, $p = .143$, whereas dropping GD did decrease Chi-square(1) = 24.6, $p < 0.0001$.

Figure 3.5



Comparison of EM and EEG effects. **A**. Eye movement behavior (FFD, GD, and refixations probability) and FRP amplitude (at Pz between 300-500 ms) is plotted across five levels of word predictability (logit scaled). Mean cloze probabilities in the five bins were .00, .01, .05, .16, and .58. Note that negative voltages are plotted upwards in this panel only. Compared to N400 amplitude, FFDs showed stronger modulations in the low than in the high predictability range. **B.** Size of the predictability effect (low minus high predictable words) in fixation times and FRPs. Each point indicates the data of one subject. Of 30 participants, 25 showed effects in the expected direction in both measures: FRPs were more negative, and fixation times were prolonged for low-predictable words. The size of EM and EEG effects did not correlate across subjects.

Psycholinguistic Discussion

In the present experiment, participants read sentences from left-to-right, while eye movements and EEG were recorded. By time-locking the EEG to fixations on words that were expected to various degrees in the sentence context, we could replicate robust effects of word predictability on behavior and concurrent brain activity. The demonstration of predictability effects in an ordinary reading situation with heterogeneous sentence materials and in- and out-going saccades suggests that EEG recordings in natural vision are feasible in principal. In this first part of the Discussion, we comment on the psycholinguistic aspects of our results. A second, methodologically-oriented part of the Discussion reviews the technical challenges that emerged in the present experiment.

N400 effects

Decreasing word predictability increased a parietal negative-going component in the FRP, that reached a maximum at 384 ms. Importantly, this effect was observed despite the limited range of cloze probabilities in the Potsdam Corpus, which contains normal sentences and mostly words of low and moderate cloze probability. Because of its time course, polarity, scalp distribution, and sensitivity to word predictability, we take this component to reflect the N400. The fact that the topography of the effect was very similar to the N400 effect commonly observed during word-by-word presentation is reassuring evidence for the ecological validity of ERP data collected in traditional SVP paradigms.

Although the present study was mainly concerned with demonstrating the feasibility of this approach and did not primarily aim at covering new psycholinguistic ground – clearly a topic for future research – it also provided one indication that co-registration may yield somewhat different results than SVP. This concerns the N400 time course: The present N400 appeared to begin earlier than what is commonly reported from SVP. In visual word presentation, N400 effects typically arise at around 200-250 ms (Kutas et al., 2006). While our conservative onset criterion yielded a latency in this range (248 ms), we also observed much weaker N400-like effect topographies in earlier intervals after fixation onset, which did not survive correction for multiple comparisons. As we did not specify mixed models for these early intervals, we cannot exclude the possibility that this pattern was due to other variables correlated with predictability (e.g. constraint). Importantly, however, such early deviations were not observed by Dambacher et al. (2006) who presented the same sentences word-by-word and tested for early predictability effects in the P200 time window. In contrast, in an unpublished follow-up experiment that used an experimental manipulation of predictability (Dimigen, Sommer, Dambacher, & Kliegl, 2008) we could

replicate the observation of a comparatively early N400 onset in natural reading. An early onset of N400 effects under natural reading conditions was also reported in a recent study by Kretzschmar, Bornkessel-Schlesewsky, & Schlesewsky (2009). These authors co-registered eye movements and EEG from centroparietal electrodes while participants read sentences that contained an entirely unpredictable target word. In a condition where the unpredictable target word was also semantically unrelated to the most expected word, an N400 effect arose soon after the first fixation on the target word (i.e., between 250-400 ms after the onset of the last *pre*-target fixation, which lasted 186 ms on average).

Although caution is necessary in the absence of a within-subject comparison to SVP, these observations indicate that the time line of word recognition in normal reading can differ from that commonly found in SVP experiments. An earlier N400 onset in normal reading is very plausible because of the parafoveal preview obtained during the previous fixation, a benefit absent in SVP. This could also explain the early N400-like deviations in the present study. But there are also other reasons why processing speed could differ in normal reading. For example, the fact that saccades are self-initiated should reduce temporal uncertainty about the arrival of new visual input. In the absence of parafoveal preview, Marton et al. (1985) still observed faster word-categorization after a 24° saccade, compared to foveal presentation. Similarly, Dimigen et al. (submitted) compared manual reaction times to small symbols presented either at fixation or at 10° eccentricity. Although parafoveal preview was unavailable in the 10° condition, post-saccadic RT (measured from saccade offset to reaction) was 30-70 ms shorter than RT to the same stimulus presented at fixation. Both results indicate that the time to prepare and execute a saccade can act as a foreperiod, which allows participants to optimize temporal preparation (e.g., Niemi & Näätänen, 1981) and thus enhances post-saccadic processing.

EM-EEG relationship

To our knowledge, the present study is the first to offer a detailed comparison of oculomotor and electrophysiological effects of a fixated item in free vision. Several exploratory analyses were carried out to investigate the EM-FRP relationship. As expected, both EM and FRP measures were sensitive to word predictability, suggesting that they are driven by common underlying processes. While gaze duration and especially refixation probability aligned well with N400 amplitude across five levels of logit predictability (Figure 3.5A), a different function was observed for first fixation durations. In an earlier study, Dambacher and Kliegl (2007) compared fixation times and ERPs for the same words, but measured in different groups of participants; EMs originated from natural reading

whereas ERPs were collected in SVP. Dambacher and Kliegl reported remarkably similar functions for the duration of single fixations and N400 amplitude across five levels of log frequency and four levels of logit predictability (their Figure 2). The profiles included even a disordinal trend with slightly longer single fixation durations and slightly larger N400 amplitude for words of medium log frequency. The study of Dambacher and Kliegl differs in several details from the present one (e.g., N400 from SVP rather than simultaneous recordings; aggregation over words, not over identical fixations) so it is difficult to speculate about the reasons for this difference in the exact relationship between fixation durations and N400 amplitude.

A model of N400 amplitude at the level of individual fixations (Table 3.3) provided no evidence for common variance between FFD and N400 amplitude that was not explained by the properties of the word or preceding sentence fragment. However, such covariance was observed between GD and N400 amplitude. Of course, this relationship could be mediated by other lexical variables not included in our model. The alternative explanation is that N400 amplitude and GD are directly related to each other, for example due to moment-to-moment fluctuations in the efficiency of word processing, which would affect both measures.

Since both EM and FRP measures are sensitive to word predictability, one might expect readers who show strong N400 effects to also show strong behavioral effects, and vice versa. For example, good readers should make better use of sentence context, and this may show up as larger predictability effects in EMs and FRPs. This was not the case: we found no evidence indicating that the size of the behavioral effects correlated with N400 effect amplitude across *participants* (Figure 3.5B). This result was surprising because Dambacher and Kliegl (2007) established such a correlation *across words* by using data from separate experiments. The lack of a correlation across *participants* is most likely caused by the notoriously unreliable difference-scores entering the correlations, which may represent too weak a signal to overcome individual differences in brain anatomy (e.g., cortical folding). Such anatomical differences between participants may influence the strength at which activity of an additional neural generator propagates to the scalp and could be a stronger source of N400 amplitude variation than differences in underlying brain activation, possibly concealing any existing relationship.

A final set of comparisons concerned the relative timing of predictability effects. Based on SVP data, it has been argued that there is a discrepancy between the latency of the N400 – the primary and so far the only robust index of semantic processing in psycholinguistic ERP research – and the fixation durations measured in eye tracking studies. The N400 typically

peaks at around 400 ms in ERP studies, a time when the eyes have already left the critical word in natural reading (Sereno & Rayner, 2003). As Rayner and Clifton (2009) have pointed out, this "conundrum" is difficult to explain: How can the eyes react faster than the brain? We were able to address this time lag question within the same dataset. Despite a relatively early N400 peak (386 ms) in normal reading, the pattern was still the same as in SVP: While predictability clearly influenced the duration of the first fixation on the target word, this fixation had almost always ended when the predictability effect peaked in the FRP (Figure 3.4D).

One common view on the N400 assumes that it reflects a late, post-lexical process of semantic context integration. Likewise, it is a commonly held view in EM research that these processes are reflected in gaze duration, which is seen as a measure of late processing. It is therefore interesting to note that the N400 peak did not fall into the mean gaze duration (278 ms) either. Of course, reading a low predictable word increases not only FFD and GD, but can also prolong later fixations on the following words (*spill-over* or *lag effects*; Rayner & Duffy, 1986; Kliegl et al., 2006). Nevertheless, the present data make it hard to conceive the measurable neural effects of predictability as being causal in some way for the behavioral effects, because the bulk of the predictability effects in ERPs only followed those in behavior. This raises questions about the functional interpretation of the N400 peak, whose latency does not seem to correspond to the maximum processing difficulty as reflected in the EM record.

Alternatively, one could consider the onset of the N400, rather than its peak, as the critical event. At the statistical N400 onset latency, readers were still looking at the target in more than half of the cases and were still in the first fixation in 38% of the cases. However, in order for lexicosemantic processing to influence FFD, it must do so before saccadic motor programming enters the non-labile stage, that is, at an estimated 80 ms before the end of the fixation (Becker, 1991; Findlay & Harris, 1984). The onset of the N400 effect therefore still seems to occur surprisingly late in comparison to the FFD effect. However, in contrast to the FRP analyses, the analyses of the SRP aligned to fixation *offset* provided some evidence that N400 effects may begin within the first fixation. The temporal contingencies observed here therefore do not rule out completely the possibility that the processes reflected in the N400 onset are also responsible for – or "driving" – the early effects in FFD. An answer to this question requires the design of dedicated experiments with strongly expected or unexpected words. Such experiments will allow very precise measurements of onset latency and possibly indicate that N400 onsets can occur early enough to influence behavior (see also Dimigen et al, 2008; Kretzschmar et al., 2009). They will also clarify

whether N400 effects can arise *before* the direct fixation of a target word due to parafoveal preview, a hypothesis that was not supported by the current results.

Possible applications

Apart from validating traditional ERP findings for more natural reading situations, co-registration can be used to investigate aspects of the reading process that are difficult or impossible to study with SVP. As described in the Introduction, one such aspect is the availability of parafoveal information in natural reading. The timing and extent to which upcoming words are preprocessed is still controversial and can be studied in greater detail with FRPs. A promising approach in this context is the combination of simultaneous recordings with gaze-contingent changes of the computer display, as they are often used in eye tracking studies to manipulate preview (e.g., the boundary technique; Rayner, 1975). The question whether word meaning can be extracted from parafoveal words is one issue that could be further investigated with this technique. Co-registration is also the only viable approach to study EEG correlates of complex reading behavior. Interesting questions concern the EEG signature before a word is skipped rather than fixated, the FRPs that precede and follow the decision to trigger a regressive saccade (and their relationship to established syntactic ERP components), or the functional localization of individual differences in reading ability and reading speed. The final section reviews the relevant technical aspects for conducting such studies.

Methodological Discussion

Researchers who wish to record the EEG during reading or other free viewing tasks are faced with several technical and data-analytical problems, which are the likely reason why such recordings have rarely been attempted. The four main challenges we identified are (1) the need for precise co-registration of gaze position (2) the correction of corneoretinal and myogenic eye movement artifacts, (3) varying degrees of overlap between successive FRPs as well as between FRPs and background ERPs, and (4) variation of saccade-related cortical potentials according to low-level visuomotor factors. In the following, we will discuss each problem and possible solutions in some detail.

Co-registration of gaze position

A basic requirement for fixation-based averaging is accurate information about the latency and location of each fixation. Traditionally, ERP researchers have used electro-oculogram (EOG, Oster & Stern, 1980) electrodes near the eyes to control for a steady fixation. Basis of

the EOG is an electrical gradient of 0.4 - 1 mV (Young & Sheena, 1988) between cornea and retina, which can be modeled by an equivalent electric dipole near the eye-ball (Berg & Scherg, 1991). Because changes in the orientation of the eye ball change the potential at peri-ocular electrodes, the EOG is well-suited to determine the onset latency of single, large saccades. However, with a spatial accuracy of ±1.5 - 2° (Malmivuo & Plonsey, 1995; Young & Sheena, 1988; see Joyce, Gorodnitsky, King, & Kutas, 2002, for a method to optimize EOG accuracy) it does not provide absolute gaze position with the single-letter accuracy required for reading analysis.

Current video-based eye trackers afford spatiotemporal resolutions up to 0.01° / 2 kHz, and both table-mounted (Bodis-Wollner et al., 2002; Baccino & Manunta, 2005; Kennett, Van Velzen, Eimer, & Driver, 2007; Hutzler et al., 2007; Valsecchi, Dimigen, Sommer, Kliegl, & Turatto, 2009; Dimigen et al., 2009; Kretzschmar et al, 2009; for MEG see Herdman & Ryan, 2007) and head-mounted (Graupner, Velichkovsky, Pannasch, & Marx, 2007; Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008) systems have been used for co-registration. Technical concerns about concurrent eye tracking are (1) pressure artifacts from contact between electrodes and eye tracker, (2) muscle artifacts resulting from head stabilization or unnatural sitting positions, (3) proper synchronization of the data records, and (4) electromagnetic artifacts from an electric device operating close to the EEG sensors. In the present study, these problems were minimized by (1) foam-cushioning forehead electrodes, (2) careful adaptation of the participant's sitting position, and (3) synchronization of EM and EEG records with a shared TTL pulse every few seconds. To double-check proper synchronization, we also use an A/D-converter in the eye tracker that feeds an analog copy of the gaze position as an additional channel into the EEG record. To test for (4) electromagnetic artifacts, we compared the EEG spectrum during steady fixation while the eye tracker was either recording or disconnected from power. We found that eye tracker operation introduced a weak 50 Hz line noise artifact at frontal electrodes near the eye tracker. However, this high-frequency artifact was irrelevant for the present FRP analyses and can be minimized by a notch filter (Yuval-Greenberg et al., 2008) or by using a remote eye tracker outside the shielded cabin.

In summary, advances in video-based eye tracking allow the routine recording of high-resolution EMs without obstructing EEG recordings. Moreover, two recent studies suggest that eye tracking can improve EEG data quality even in experiments that require steady fixation, as it allows to identify myogenic (Yuval-Greenberg et al., 2008) and visuocortical (Dimigen et al., 2009) potentials from involuntary microsaccades.

Eye movement artifacts

Eye movement artifacts in the EEG are generated by three mechanisms: rotation of the eye ball's corneoretinal dipole (Berg & Scherg, 1991), relative movements of the eye lid during blinks and upwards saccades (Picton et al., 2000), and electrical eye muscle activity at saccade onset, which propagates to the EEG as a spike potential (Thickbroom & Mastaglia, 1986). In normal vision, the strongest artifact source are corneoretinal artifacts. The changes in the corneoretinal potential, which provide the basis for the EOG, also propagate to the EEG electrodes, although they attenuate with increasing distance to the eyes (Picton et al., 2000). The horizontal saccades that are dominant in reading produce largest distortions at lateral-frontal channels and smallest distortions at posterior electrodes along the sagittal midline. While excluding of contaminated trials is not an option during natural vision, there are simple ways to minimize EEG contamination despite saccades. Early studies with saccades recorded only from occipital midline sites (e.g., Gaarder, Krauskopf, Graf, Kropfl, & Armington, 1964) or used equal numbers of left- and right-going saccades, based on the assumption that both artifacts cancel out during averaging (e.g., Kurtzberg & Vaughan, 1981; Marton, Szirtes, & Breuer, 1985). Others have avoided the problem by limiting data analyses to the short interval of EEG before the first saccade (Baccino & Manunta, 2005; Simola et al., 2009) or after the terminal saccade in a sequence of saccades (e.g., Hutzler et al., 2007; Marton & Szirtes, 1988a; 1988b). Obviously, these approaches place severe limitations on the time segment, electrode site, and study design.

A large variety of algorithms have been proposed to correct mathematically for ocular artifacts (for reviews see Brunia et al., 1989; Gratton, 1998; Croft & Barry, 2000; Ille et al., 2002; Delorme, Sejnowski, & Makeig, 2007). Interestingly, the application of these algorithms has been largely restricted to correcting blink artifacts and accidental saccades in experiments that require fixation. Here, we applied surrogate MSEC (Berg & Scherg, 1994; Ille et al., 2002) to correct the heavily contaminated data. Although the collection of clean calibration EMs from each subject is time-consuming, the method was chosen for four reasons. First, MSEC can reduce the elimination of genuine brain activity compared to traditional regression-based methods (Berg & Scherg, 1994), because brain activity is modeled. Second, MSEC can be applied to continuous rather than averaged data, which supports a flexible re-segmentation of the corrected EEG to different time-locking points (e.g., the onset of fixation *n*-1). Third, the method does not make assumptions on the spatial or temporal orthogonality or independence of artifact and brain activities (the application of PCA during preprocessing is optional). Fourth, it does not require subjective choices from the experimenter apart from the one-time selection of a surrogate brain model.

Inspection of the continuous EEG, analysis of the averaged FRP, and analysis of residual correlations with the eye tracker converged to suggest that it was feasible to compensate for most of the artifact. While artifacts from the incoming saccade were completely abolished, residual artifact remained towards the very end of the fixation-locked segment, when several saccade artifacts had summated. This became apparent as small but significant correlations between about half of the corrected EEG channels and the eye track. Also, MSEC did not fully remove the spike potential (cf. Figure 3.4A, right panel), because its topography was not pre-defined as an artifact source. In summary, residual artifacts were small and correction quality was sufficient for the analyses that were being conducted. The use of more electrodes and a more realistic surrogate model may further improve MSEC correction.

Utility of eye tracking to improve ocular correction

Although correction worked well for the present purposes, other algorithms may have performed equally well or better. However, a fundamental problem with ocular correction methods is a lack of objective external criteria (Brunia et al., 1989) to compare and evaluate their performance on experimental data (for simulated data see Delorme et al., 2007; Klemm, Haueisen, & Ivanova, 2009; Wallstrom, Kass, Miller, Cohn, & Fox, 2004). Choice of an appropriate correction method is particularly important for natural vision recordings. We therefore propose that concurrent eye tracking is useful to evaluate, compare, and improve correction methods:

First, unlike the EOG, the eye track provides a measure of eye position that is electrically independent of the EEG. Correlations between eye track and EEG after correction are therefore likely to result from residual corneoretinal or myogenic artifacts (or, less likely, from saccade-related brain activity occurring in synchrony with the saccade). The degree to which the EEG depends on eye position after correction (exemplified here by a linear correlation) can help to evaluate correction quality across studies and algorithms.

Second, eye tracking may inform about whether an algorithm overcorrected the data and distorted genuine brain activity. Provided that an experiment contains at least some intervals with steady fixation, high-resolution eye tracking allows the researcher to select EEG intervals *objectively* free of any ocular artifact (eye blinks, saccades, and microsaccades). These intervals should not be altered by ocular correction and therefore provide a test-case to quantify the distortion of brain signals introduced by the method.

Third, eye tracking may directly improve correction. Correction methods based on PCA or independent component analysis (ICA) decompose the EEG into multiple uncorrelated

(e.g., Lagerlund, Sharbrough, & Busacker, 1997) or statistically independent (Delorme et al., 2007) signal components and correction is then performed by removing components classified as artifact. This classification is typically performed manually and based on criteria such as the component's scalp distribution and spectrum (Rong & Contreras-Vidal, 2006; Okada, Jung, & Kobayashi, 2007; Li, Ma, Lu, & Li, 2006), or correlation with the EOG (Joyce, Gorodnitsky, & Kutas, 2004; Wallstrom et al., 2004). However, classification can be ambiguous, especially when many components are produced, and many studies do not report selection-criteria (Fatourechi, Bashashati, Ward, & Birch, 2007). Considering the relationship between the components' time series and gaze position (i.e., eye tracker-informed ICA) should greatly improve the reliability of component selection.

Finally, we propose that ocular correction is entirely unnecessary for certain research questions. Reading studies with SVP have provided some evidence of early ERP correlates of lexicosemantic processing within 200 ms after stimulus onset (Dambacher, Rolfs, Göllner, Kliegl, & Jacobs, 2009; Penolazzi, Hauk, & Pulvermüller, 2007; Hauk & Pulvermüller, 2004; Sereno, Brewer, & O'Donnell, 2003; for review see Pulvermüller, Shtyrov, & Hauk, 2009). An interesting question will be whether similar effects, within the duration of the current fixation, can be reliably established in FRPs and whether they predict the current fixation duration or the upcoming saccade target. Each fixation, however, is by definition a short interval of EEG that is free of EMs and that can be analyzed without prior correction. This approach requires a sufficient number of fixations with a minimum duration (e.g., 200 ms) after shorter fixations have been excluded. Second, because the artifact of the incoming saccade precedes fixation onset, a pre-fixation baseline - as in the present study - is not feasible. Instead, the baseline could be placed in the first few milliseconds of the fixation itself (provided that effects are not already present in the baseline due to parafoveal preview). Finally, direct current (DC) amplifiers should be used to prevent a spill-over of the pre-fixation artifact into the post-fixation segment due to the amplifier's time constant (Yagi, Kazai, & Takeda, 2000).

In summary, results suggest that corneoretinal artifacts are not a principal - and not the most serious - obstacle for EEG recordings during natural vision: Correction was sufficient for the present analyses and can likely be improved further. Eye tracking provides new criteria to validate and optimize correction while certain analyses do not require artifact correction at all.

Differential overlap

Serial presentation allows full control over the stimulus that is presented to the visual system at any time. In normal vision, on the other hand, the experimenter has little control over the spatio-temporal pattern of fixations, in particular over the latency and duration at which a participant chooses to fixate a target item. This leads to two problems of EEG overlap:

The first problem is the varying degree of temporal overlap between the potentials evoked by a target fixation and existing EEG *background activity* that is related, for example, to the stimulus onset. In the present experiment, sentence onset evoked a P300, which returned to baseline level only after about 700 ms. If target items in two conditions are fixated at systematically different latencies after stimulus onset – for example salient versus non-salient parts of a picture during scene perception – fixation-related potentials occur against a different background. This will distort the FRP waveshape and topography between conditions[18]. It is therefore important to ensure that target fixations do not differ in terms of overlapping background activity. In the current case, this was done by excluding early fixations and by ensuring that the pre-fixation baseline activity did not differ between predictability levels.

The second problem is temporal overlap between the potentials elicited by *successive reading fixations*. With inter-fixation intervals of around 250 ms, reading proceeds considerably faster than typical SVP paradigms, leading to massive overlap between the potentials evoked by subsequent fixations. This means that late, endogenous components from the previous fixation *n-1* overlap early, exogenous components from fixation *n*. Likewise, late components from *n* will overlap early components from *n+1* (cf. Figure 3.2B). Temporal overlap and, hence, summation of successive fixation-related responses over the duration of the trial was also the likely reason for the highly significant effect of word position on EEG amplitude in the N400 window (see Table 3.3); an effect that did not reach significance when the same sentences were presented in SVP (Dambacher et al, 2006).

[18] Consider this example: In normal sentences, low predictable words tend to occur at earlier word positions and will be fixated sooner after sentence onset. As a consequence, the pre-fixation baseline interval for these fixations will overlap more often with the sentence-evoked P300. Via the process of baseline correction, which involves the subtraction of the baseline voltage from each channel, the sentence-onset P300 (a centroparietal positivity) will carry over into the fixation-locked segment with a reversed polarity (as a centroparietal negativity), thereby creating a bogus, N400-like effect for low predictable words.

Due to variance in fixation duration, the overlapping potentials will be latency-jittered relative to the current fixation and therefore low-pass filtered (Woldorff, 1993). While overlap is also encountered in fast SVP experiments (which have presented words at up to 10 Hz; Kutas, 1987), overlap is problematic if it differs systematically between conditions. This is clearly the case in reading and many other viewing tasks, where readers modulate fixation time according to processing difficulty. Because any fixation duration effect translates into a change in the phase of the overlapping potentials, EEG effects that reflect stimulus processing can be easily confused with changes that merely result from different degrees of overlap. Because differential overlap occurs with any fast and self-paced stimulation, the problem also applies to self-paced SVP (Ditman, Holcomb, & Kuperberg, 2007).

The extent to which overlap is a problem depends on the exact paradigm and the size of the behavioral effect. For example, the last fixation in a sequence is only influenced by overlap from previous fixations but not from subsequent fixations. In addition, in the absence of behavioral effects on fixation *n-1* (e.g., a parafovea-on-fovea effect), different overlap will influence the FRP only after the outgoing saccade is executed (this is not entirely true, because correlates of saccade preparation like the pre-saccadic positivity may precede the outgoing saccade).

We are not aware of a simple solution to the problem of differential overlap in FRPs, and this problem has been ignored in previous SRP/FRP studies. Several deconvolution methods have been proposed to separate overlapping potentials in ERP experiments with fast stimulation and variable inter-stimulus intervals (Woldorff, 1993; Jewett et al., 2004; Wang et al., 2006; Hansen, 1983; Delgado & Özdamar, 2004). For example, *ADJAR* (level 2 implementation, Woldorff, 1993) is a time-domain technique that iteratively deconvolves overlapping waveforms based on knowledge about the temporal distribution of the ERP-eliciting events. In natural vision, this information is provided by the eye tracker. However, deconvolution methods typically rely on high signal-to-noise ratios (Talsma & Woldorff, 2004), require knowledge about the non-overlapped template waveform, or make the assumption that each successive event evokes an identical response. As discussed in the next section, the last condition, in particular, is unlikely to be met during free vision and it needs to be tested whether deconvolution can be successfully applied to FRPs.

However, the influence of differential overlap can at least be approximated by convolving an estimate of the non-overlapped FRP with the latency distribution of fixation onsets in

each condition (here: low, medium, and high predictable words)[19]. As an alternative, the large pool of fixations that is easily obtained during natural vision allows the selection of fixation subsamples from each condition that are matched in terms of fixation duration. Because experimental effects on fixation duration are often small in reading, only a small percentage of fixations must be excluded to equalize the distribution of fixation durations post-hoc. Obviously, the resulting fixation samples, matched for fixation duration, present a biased selection, which may exclude the theoretically most interesting fixations. However, this procedure provides a simple test whether FRP effects persist once overlap is controlled.

Low-level influences on saccade-related brain potentials

Saccade- and fixation-related brain potentials are not only modulated by higher cognitive processing demands, but their waveshape is also influenced by visuomotor low-level factors that cannot be controlled during natural scanning behavior. These influences must be carefully delineated from effects that reflect higher-level cognitive processing (e.g., semantic processing) of the fixated item. Among these low level influences are (1) the exact visual input at saccade offset, and (2) the kinematics of the incoming saccade.

Most ERP studies of higher cognitive processing invest great care to match their visual stimuli in terms of low-level properties such as contrast, luminance, and spatial frequency. In contrast, retinal inputs vary considerably across different fixation locations (e.g., the center vs. the edge of a bright screen). Both amplitude and latency of the visually-driven lambda response around 100 ms after fixation onset (cf. Figure 3.2) vary as a function of the luminance and contrast (Gaarder et al., 1964; Kazai & Yagi, 1999; 2006; Marton & Szirtes, 1982) and spatial frequency (Kazai & Yagi, 2006; Armington & Bloom, 1974) of the background. The lambda response therefore resembles the P1 component in ERPs, which is generated in overlapping areas of visual cortex (Kazai & Yagi, 2003) and modulated by the luminance, size, contrast, and frequency content of the field of presentation (Tobimatsu & Celesia, 2006). Visual influences on the lambda response have been observed with stimuli that covered large parts of the visual field (Riemslag et al., 1987). To our knowledge, no study has investigated the question whether differences in the foveal input across different fixation locations – for example local changes in luminance and contrast when viewing

[19] Such a simulation (not shown here), conducted for the present dataset with the grand-average FRP (averaged across conditions) as the waveform estimate, suggested that effects of differential overlap were small compared to the much larger effect of word predictability.

different parts of a scene - cause relevant modulations of the fixation-related EEG. For the sentence stimuli presented in the current study, we assumed that visual field properties would be comparable for different fixation locations on the screen. In addition, we attempted to reduce purely visually-driven effects by covering the peripheral visual field with a mask.

A second important low-level factor that influences SRPs and FRPs is saccade size. Saccade amplitude modulates not only the size of the pre-saccadic muscle spike (Boylan & Ross Doig, 1989), but also the waveshape of the post-saccadic EEG. The visual lambda response, in particular, comprises both saccade onset- and saccade offset-related responses (Thickbroom et al., 1991; Kurtzberg & Vaughan, 1977). For long saccades (> 10°), it dissociates into two subcomponents, a first subcomponent, presumably related to visual changes at saccade onset and a larger second one, presumably evoked by the inflow of new visual input at saccade offset (Thickbroom et al., 1991). However, as Figure 3.2C shows, saccade amplitude modulates the lambda response even for the limited range of saccade amplitudes found in reading. Therefore one needs to be cautious when conditions are compared that differ in terms of incoming saccade amplitude. This is not necessarily a fundamental limitation because reading saccades have fairly constant amplitudes of around 7-9 characters (Rayner, 1998) and eye tracking allows the post-hoc exclusion of very short or long saccades. In the present case, condition differences in incoming or outgoing saccade amplitude were too small (< 0.1°) to cause relevant changes in FRP waveshape. However, when we specified an mixed model (not shown here) in which we added incoming saccade amplitude as an additional predictor, this predictor explained EEG variance at electrode Pz in all time windows between 40 and 280 ms after fixation onset. We therefore propose to include incoming saccade amplitude as a covariate in FRP analyses. Finally, we are not aware of any study that has tested the influence of saccade *direction* on FRPs, a question that seems important for applications of the technique to visual search or scene perception.

Summary: Feasibility of co-registration

Fixation-related potentials are influenced by corneoretinal artifacts, differential overlap, and visual- and motor-related brain potentials, all of which vary with oculomotor behavior. These indirect influences of EM behavior on the EEG can be easily mistaken for genuine condition differences in the brain's processing of the fixated item. Special care must be taken during the analysis and interpretation of multi-saccadic EEG experiments, and researchers should account for how these problems were addressed. In particular, details

about oculomotor behavior (fixation durations and saccade amplitudes) on the fixations preceding and following a target fixation should be provided. The aforementioned problems are not exclusive to the analysis of FRPs in the time domain but also apply to EEG analyses in the frequency domain, that is, to saccade- or fixation-related oscillations (SROs or FROs). However, EEG recordings in natural vision also have the major advantage in that many fixations can be collected in a short time and with little strain on the subject. In future studies, these large fixation pools could be used to model and disentangle the influences of artifacts, low-level processing, and higher level processing on the fixation-related EEG.

Conclusions

Visual perception outside the ERP laboratory is fundamentally trans-saccadic and involves an active sampling of the environment several times per second. What types of information are obtained on each fixation and how is it integrated with the information from previous and subsequent fixations? Despite their advantages, EEG recordings have been largely precluded from natural viewing conditions. We demonstrated here that EEG indices of semantic processing can be obtained in natural reading and compared to EM behavior. With the appropriate consideration of technical and data-analytic issues, concurrent recordings may contribute new answers to long-standing questions.

Acknowledgements

Funding was provided by grants from Deutsche Forschungsgemeinschaft (KL 655/6 and FOR 868). Results were first presented at the International Conference on Cognitive Neuroscience (2005) and the 13th Meeting of the Cognitive Neuroscience Society (2006). The authors thank Petra Grüttner for assistance in data collection, Rainer Kniesche for technical support, Mark Minnes for proof reading, and Tim Curran and three anonymous reviewers for their helpful comments.

4. Trans-saccadic parafoveal preview benefits in fluent reading: A study with FRPs[20]

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Abstract

During natural reading, a parafoveal preview of the upcoming word facilitates its subsequent recognition (e.g., shorter fixation durations compared to masked preview) but nothing is known about the neural correlates of this so-called preview benefit. Furthermore, while the evidence is strong that readers preprocess orthographic features of upcoming words, it is controversial whether word meaning can also be accessed parafoveally. We investigated the timing, scope, and electrophysiological correlates of parafoveal information use in reading by simultaneously recording eye movements and fixation-related brain potentials (FRPs) while participants read word lists fluently from left to right. For one word – the target – (e.g., "*blade*") parafoveal information was manipulated by showing an identical ("*blade*"), semantically related ("*knife*"), or unrelated ("*sugar*") word as preview. In *boundary trials*, the preview was shown parafoveally but changed to the correct target word during the incoming saccade. Replicating classic findings, target words were fixated shorter after identical previews. In the EEG, this benefit was reflected in an occipitotemporal *preview positivity* between 200-280 ms. In contrast, there was no facilitation from related previews. In *parafoveal-on-foveal* trials, preview and target were embedded at neighboring list positions without a display change. Consecutive fixation of two related words produced N400 priming effects, but only shortly (160 ms) after the second word was directly fixated. Results demonstrate that neural responses to words are substantially altered by parafoveal preprocessing under normal reading conditions. We found no evidence that word meaning contributes to these effects. Saccade-contingent display manipulations can be combined with EEG recordings to study extrafoveal perception in vision.

[20] published in 2012 in *Neuroimage, 62*, 381-393

Introduction

Readers sample each line of text with a series of eye fixations connected by rapid, jerk-like eye movements (EMs), called saccades. While useful visual input is only obtained during fixations (typically lasting 180-250 ms), saccades serve to move new text into the fovea, the central part of the visual field, covering 1-2°. The sharp drop-off in retinal acuity outside the fovea and visual crowding (Pelli et al., 2007) limit the amount of information that readers can extract from parafoveal and peripheral words (Rayner, 1998).

The question of how much information readers extract at which point in time from not-yet-fixated words is a central issue in reading research (Rayner, White, Kambe, Miller, & Liversedge, 2003). Over the last 35 years, eye tracking studies have gathered strong evidence that readers take up information not only from the currently fixated word, but also from upcoming words in the direction of reading (McConkie & Rayner, 1975; Rayner, 1975). While these studies suggest that extrafoveal preprocessing is a fundamental aspect of word recognition under natural reading conditions, the brain correlates of reading have almost exclusively been studied in the absence of oculomotor behavior and parafoveal information (Kutas, Van Petten, & Kluender, 2006). Consequently, little is known about the neural dynamics of the actual reading process and the impact of parafoveal preprocessing on brain systems involved in word recognition (Sereno & Rayner, 2003).

Furthermore, while there is general agreement that readers extract some information from upcoming words, it is controversial whether preprocessing is limited to low-level features and sub-lexical information or whether it extends to lexico-semantic properties. The present study investigated the electrophysiological correlates and scope of parafoveal processing in fluent reading by combining a recently established method for EEG analysis - the recording of fixation-related potentials (FRPs, Dimigen, Sommer, Hohlfeld, Jacobs, & Kliegl, 2011) – with experimental techniques from eye movement research.

Eye tracking studies on parafoveal processing have mostly used the *Boundary Paradigm* (Rayner, 1975). In this paradigm, one target word in a sentence (henceforth called word n+1) is masked by an uninformative preview string, for example an unrelated word of the same length. Only during the saccade from the preceding word n to word n+1, once the eyes cross an invisible boundary on the screen, the preview is changed to the correct target word. Because visual thresholds are elevated during saccades (Ishida & Ikeda, 1989; Matin, 1974) readers usually remain unaware of this manipulation (Slattery, Angele, & Rayner, 2011).

The benchmark finding obtained in this paradigm is the *identity preview benefit*: After valid (identical) previews, target fixations are 20-50 ms shorter than after uninformative previews. By varying the preview-target relationship, EM studies have shown that readers still benefit from preview when the word's visual features change during the saccade (i.e., the preview "ROUGH" facilitates "rough"; Inhoff, Starr, & Shindler, 2000; McConkie & Zola, 1984; Rayner, McConkie, & Zola, 1980) or when preview and target are not in the exact same physical location (Rayner, McConkie, & Ehrlich, 1978). This suggests that the benefit is not primarily based on a trans-saccadic fusion of visual low-level features. Instead, it has been proposed that readers extract more sparse and abstract representations, in particular case-independent letter identities and orthographic codes from the initial two or three letters (Rayner, 1998; Rayner et al., 2003) of the upcoming word. In addition, some benefit is observed after phonologically related (homophone) previews (Chace, Rayner, & Well, 2005; Henderson, Dixon, Petersen, Twilley, & Ferreira, 1995; Pollatsek, Lesch, Morris, & Rayner, 1992).

A neural correlate of trans-saccadic preview benefit?

Studies with event-related potentials (ERP) have investigated visual word recognition in great detail (Barber & Kutas, 2007; Kutas et al., 2006; Pulvermüller, Shtyrov, & Hauk, 2009) but rarely during actual fluent reading. Instead, stimuli are usually presented as a comparatively slow stream of isolated words while subjects fixate the screen center. In natural reading, on the other hand, typical preview benefits correspond to a reduction of 5 to 25% of the fixation time spent on a word. Assuming that fixation times are a reasonable approximation of the duration of the underlying word recognition process, this suggests that preview could have a profound impact on the time course and morphology of psycholinguistic ERPs.

The first goal of the present study was therefore to identify an EEG correlate of the preview benefit present under fluent reading conditions. The EM literature affords several hypotheses about functional loci and neural correlates of the identity preview benefit. Given its reported robustness against changes in low-level features, we hypothesized that EEG effects should not primarily manifest on the earliest stages of visual processing (up to and including the visual P1 component, peaking at around 100 ms). Instead, preview might modulate the N400, a centroparietal-negative ERP component sensitive to various types of foveal priming, including masked priming by full or partial word repetitions (Holcomb & Grainger, 2006, 2007). However, with a peak around 400 ms, the N400 seems to occur too late to be a neural equivalent (i.e., a causal predecessor) of changes in oculomotor

measures (Dimigen et al., 2011; Rayner & Clifton, 2009), because EM benefits are already observed during the first fixation on a previewed word (e.g., Rayner, Balota, & Pollatsek, 1986; White, Rayner, & Liversedge, 2005). This led us to hypothesize that (a) some neural correlate of preview should be measurable within a typical fixation duration (i.e., within 180-250 ms or less, considering delays needed to program the next saccade) and (b) identity previews might influence ERP components in a middle latency range - such as the occipitotemporal N1 component - which are often linked to mid-level vision, orthographic processing, and early word form processing in the ventral stream.

Do readers access parafoveal word meaning?

Whereas benefit has been demonstrated for orthographically and phonologically related previews, there is debate whether readers also extract semantic codes parafoveally (Rayner et al., 2003). In such a case, readers should benefit from semantically associated parafoveal prime words (e.g., the preview "tune" should shorten subsequent fixations on "song"). Recently, evidence for such semantic preview benefit was reported for reading Chinese (Yan, Richter, Shu, & Kliegl, 2009) and German (Hohenstein, Laubrock, & Kliegl, 2010). Furthermore, there is evidence for semantic preview benefit between the constituents of long Finnish compound words (White, Bertram, & Hyönä, 2008). However, other boundary studies found no changes in fixation time following semantically related previews (Altarriba, Kambe, Pollatsek, & Rayner, 2001; Rayner et al., 1986) or previews consisting of emotionally arousing "shock words" (Hyönä & Häikiö, 2005). The existence of a semantic preview benefit and the boundary conditions under which it occurs therefore remain controversial[21].

ERPs are highly sensitive to semantic priming (Kutas & Federmeier, 2011) and the issue of parafoveal semantics has been investigated in several stimulus-locked ERP studies. Importantly, these studies did not use display changes but tested for *parafoveal-on-foveal* effects (POF, Kennedy, Pynte, & Ducrot, 2002). In principle, if parafoveal information becomes rapidly accessible, features of an upcoming target word could also be reflected in fixation times or EEG measures while the eyes still rest on the word *before* the target. A POF effect is therefore defined as any influence of the properties of the next word *n*+1 that arises while the reader is still fixating word *n*. Therefore, the boundary paradigm

[21] The fact that readers often skip short function words (e.g. "the") demonstrates that words can be identified without a direct fixation if they are fully predictable from the context. It is controversial whether readers extract semantics from parafoveal content words that are subsequently fixated (rather than skipped, see Rayner et al., 2003 for a discussion) and only such cases are analyzed here.

investigates the *consequences* of having had a preview for a given word that is now being fixated, whereas POF effects reflect immediate influences of information about a word that is still in the parafovea on the processing of the currently fixated word. These different but complementary approaches can be combined to obtain a full picture of preprocessing effects.

Like EM studies, ERP studies have produced partially conflicting results. Two studies (Baccino & Manunta, 2005; Simola, Holmqvist, & Lindgren, 2009) presented word pairs that were associated or non-associated in meaning. The first word was presented in the screen center, flanked parafoveally by the second word. ERPs were time-locked to word pair onset and analyzed up to the moment that participants initiated a saccade to the parafoveal word. Baccino and Manunta reported an effect of semantic association on the ERP within 215 ms after stimulus onset (but found no effect on behavior), indicating that parafoveal word meaning was retrieved to some extent. However, Simola and colleagues did not replicate a semantic POF effect under similar conditions.

Another recent approach has been to adapt traditional serial visual presentation (SVP) by moving a whole sentence word-by-word across the screen while participants keep a central fixation (Barber, Ben Zvi, Bentin, & Kutas, 2010; Barber, Donamayor, & Kutas, 2010). Interestingly, this paradigm revealed congruency effects in the ERP when a parafoveal word mismatched a highly predictive sentence context (Barber, Van der Meij, López-Perez, & Kutas, 2011, see also Kretzschmar, Bornkessel-Schlesewsky, & Schlesewsky, 2009). However, this congruency effect is not necessarily semantic in nature, since strong expectancies (and slow presentation speeds in some of the studies) may have allowed participants to determine the contextual fit of the upcoming word based on partial orthographic information. More generally, it is difficult to generalize results from SVP to fluent reading. While participants in SVP studies have no incentive to shift or bias attention towards extrafoveal regions, readers shift attention to the saccade target as a part of oculomotor preparation (Hoffman & Subramaniam, 1995). On the other hand, stimulus on- and offsets in SVP can artificially increase the salience of parafoveal words.

Present study

A novel approach that bridges the methodological gap between EM and EEG studies is to align the EEG signal to fixation onsets in free viewing situations. Importantly, the technical and data-analytical challenges associated with this technique (e.g., corneoretinal artifacts, overlapping potentials) can be addressed by a combination of correction methods and careful post-hoc analyses (see Dimigen et al., 2011 for a review) and large psycholinguistic

effects in the N400 time range have already been successfully replicated in fixation-related potentials (Dimigen et al., 2011; Hutzler et al., 2007; Kretzschmar et al., 2009; see also Marton, 1991).

In the present study we used FRPs to test the impact of identity previews and semantic previews on word recognition during fluent reading. Participants read lists of German nouns at their own pace from left to right. For one word in the list (e.g. "Frau", *woman*) parafoveal information was manipulated by showing one of three alternative previews: a valid identical preview ("Frau"), a semantically related preview (e.g. "Dame", *lady*), or an unrelated preview (e.g. "Wald", *forest*). Effects were analyzed simultaneously in fixation times and FRPs and both as preview benefits and as POF effects. The resulting 3 × 2 design is illustrated in Figure 4.1: Half of the trials used the boundary paradigm. A classic EM benefit with as yet unknown correlates in the EEG was expected after identical previews as compared to unrelated ones. In addition, any difference in behavior or EEG following related versus unrelated previews would support the existence of semantic preview benefit. The other half of trials used the POF paradigm. Here, preview and target were simply embedded at neighboring list positions (again called *n* and *n*+1) without a display changes (Baccino & Manunta, 2005; Simola et al., 2009). If meaning is extracted parafoveally, a semantic relation between word *n* and *n*+1 should influence fixation times or FRPs while the reader is still looking at word *n*. In any case, FRPs should reveal the exact point in time when word meaning becomes available to the reader.

Method

Participants

Thirty-five participants (24 woman, age 19 to 36, *M* = 24.4 years) entered the analyses. Data of one additional participant was excluded because of EEG voltage drifts. Participants were native German speakers with uncorrected vision and normal acuity (as tested prior to the experiment; Bach, 1996). According to Oldfield's (1971) questionnaire, 31 participants were right-handed and four were ambidextrous (laterality quotient: *M* = +88). Participants received 20 € or course credit for participation.

General task

To approximate a normal reading flow, target words and their previews were embedded in lists of other nouns, here called "fillers". The reading of word lists (Hutzler et al., 2007; Kennedy et al., 2002; Schroyens, Vitu, Brysbaert, & d'Ydewalle, 1999) offers excellent

control over behavioral covariates (e.g. incoming saccade amplitude, Dimigen et al., 2011) that can complicate FRP analysis during sentence reading. Each list consisted of five words. The task of the participant was to indicate after each trial whether or not the list contained the name of an animal (see *Procedure* for details). This semantic decision (e.g., Grainger, Kiyonaga, & Holcomb, 2006) discourages superficial scanning strategies and ensures that participants read for understanding.

Construction of word lists

Filler words were drawn from a pool of 1,248 German nouns with four to six letters (*M* = 5.2, *SD* = 0.8). Their mean type frequency, retrieved from the 100-million word DWDS corpus (accessible via http://dlexdb.de; Heister et al., 2011) was 12.3 per million (*SD* = 38.0). Preview manipulations occurred at two possible locations within the five-word list. In boundary trials, word *n*+1 was located at list position two or four; the preceding filler at position one or three, respectively, functioned as word *n* (i.e., as the word from which the preview on word *n*+1 is obtained). Please note that the labels *n* and *n*+1 therefore only refer to the relative positions of the two critical words within a given list, regardless of their absolute list positions. To facilitate parafoveal processing (Henderson & Ferreira, 1990), the filler word at position *n* was at least of medium frequency (*M* = 46.3, *SD* = 73.3). Its length was equiprobably four, five, or six letters (*M* = 5.0).

In POF trials, words *n* and *n*+1 were embedded either at positions two and three or at positions four and five in the list (thereby replacing the filler word at position *n*). The relevant word to investigate preprocessing effects (*n*+1 in boundary trials, *n* in POF trials) was therefore always located at list position two or four. Please note that in POF trials with an identical preview, the same word was repeated at positions *n* and *n*+1.

Preview-targets pairs

The basis for the construction of target nouns and their preview nouns was a set of 312 pairs of semantically associated German nouns (e.g. “Frau” – “Dame”, *woman* – *lady*; or “Wald” – “Baum”, *forest* – *tree*). Pairs were selected from a larger set of pairs after a semantic rating (see below). The nouns of each pair had the same length (between 4-7 letters, *M* = 5.4) and were either synonyms, associatively related, conceptually related (e.g., part-whole relation), or both associatively and conceptually related. Additionally, pairs included a few strongly associated antonyms (e.g., “Ebbe” – “Flut”, *ebb tide* - *high tide*). Mean word frequency was 31.6 (*SD* = 54.0) for previews and 19.2 (*SD* = 40.1) for targets. A full list of pairs is provided in Appendix A.

From these 312 related pairs, 312 unrelated pairs were created by exchanging the previews of two pairs with the same word length, yielding two new pairs without noteworthy semantic associations *(woman – tree, forest – lady).* In the identical preview condition, the target word served as its own preview (*tree – tree*, *lady – lady*). Thus, for example, the target word *lady* had *woman*/*forest*/*lady* as possible previews and *tree* had *forest*/*woman*/*tree* as previews (in German all of these words have the same length). In the following, such a set of two related word pairs, their two unrelated recombinations, plus their identical previews is called "preview-target unit".

Semantic rating

In a pre-experiment, all pairs of the preview-target units were rated for association strength. Fifteen native German-speaking university students (13 women, M = 27.4 years, range: 20-43 years) used a scale from 1 to 5 on a keyboard to indicate how related both words are. In each trial, the two nouns appeared next to each other on the midline of the screen in the same font as in the experiment proper. Related and unrelated pairings were presented in random order and participants were asked to give their first, spontaneous impressions (mean RT = 2.2 s).

With a mean score of 4.50 (*SD:* 0.34), related pairs were rated as significantly more related than their recombinations, $t(311) = 129.1$, $p < .0001$, which received a mean score of 1.52 (*SD*: 0.26). In addition, all preview-target units fulfilled the following criteria: (1) both related pairs scored > 3.5, (2) both unrelated pairs scored < 2.5, and (3) the two related differed from the two unrelated pairs by > 1.5 points.

As an additional measure of semantic association, we computed collocation norms for all pairs from the DWDS corpus. The resulting measure, *Mutual Information* describes the likelihood that two words co-occur within the same sentence of a text corpus. As expected, Mutual Information (logarithmized to base 10) was higher for related than for unrelated pairs, M = 5.12 vs. 4.71, $t(311) = 10.5$, $p < .0001$.

Table 4.1. Similarity measures for related and unrelated preview-target pairings

Similarity measure	related	unrelated	*p*	
Semantic				
Association rating (*N* = 15)	4.50	1.52	0.00	***
Mutual Information (log10)	5.12	4.71	0.00	***
Visual				
Letters with matching stroke direction (%)	66	66	0.77	*n.s.*
Visual confusability, letter 1	0.26	0.26	0.92	*n.s.*
Visual confusability, letters 2 & 3	0.07	0.06	0.65	*n.s.*
Visual confusability, mean of all letters	0.11	0.11	0.53	*n.s.*
Orthographic (position-specific)				
Same letter 1 (%)	0	0	--	*n.s.*
Same letter 2 (%)	8	8	1.00	*n.s.*
Same final letter (%)	15	15	0.89	*n.s.*
Hamming distance	4.89	4.89	1.00	*n.s.*
Orthographic (position-invariant)				
% of bigrams shared	11	10	0.74	*n.s.*
% of trigrams shared	1	1	1.00	*n.s.*
Dice's coefficient (bigram-based)	0.04	0.04	0.78	*n.s.*
Phonological				
Same phoneme 1 (%)	0	0	--	*n.s.*
Same phoneme 2 (%)	3	4	0.25	*n.s.*
Same final phoneme (%)	15	15	0.89	*n.s.*
Levenshtein distance (phoneme-based)	4.63	4.68	0.44	*n.s.*

Note: Given are means across words. Similarity measures and the matching procedure are explained in Appendix A.

Non-semantic matching

For the experiment, it is crucial that any differences between the related and the unrelated preview condition can be unambiguously attributed to semantic processing. Since both conditions used the same words, lexical properties such as word frequency were matched. Nevertheless, it is possible that semantically related words are more similar to each other than unrelated words on visual, orthographic, phonological, or syntactic dimensions. To rule out priming based on non-semantic properties, preview and target never started with the same letter or phoneme. In addition, related pairs were matched to unrelated pairs on

19 non-semantic measures of word similarity (see Table 4.1, see also Appendix A for details).

Balancing

To avoid word repetition, a given participant was presented either with the two related (Frau-Dame and Wald-Baum), the two unrelated (Frau-Baum and Wald-Dame), or the two identical combinations (Dame-Dame and Baum-Baum) of a given unit. These two pairings viewed by a given participant were embedded in different lists of fillers. As a result, no filler, preview, or target was ever repeated during the experiment (except, of course, for the immediate word repetition in POF trials with an identity preview).

Lists were constructed with the aim of minimizing orthographic, phonological, and semantic overlap between fillers and the embedded words of the preview-target unit. Fillers never started with the same letter and were orthographically dissimilar (all Dice coefficients < 0.5; Lambert, Donderi, & Senders, 2002) to the words of the embedded preview-target unit. Furthermore, high collocation values between fillers and previews/targets were avoided. Across participants, it was balanced whether a particular list was presented in the related, identical, or unrelated condition, whether it was shown in the boundary or POF paradigm, and whether the manipulation occurred at the early or late list position. During the experiment, lists belonging of all experimental conditions were presented randomly intermixed (i.e., boundary trials and POF trials were also intermixed).

Animal lists

Remaining fillers were used to create 60 additional lists which contained the name of an animal equiprobably at one of the five list positions. The embedded animal names had a length of 4-6 letters, a mean lemma frequency of 4 (SD = 5), and included both common (e.g., “Schaf”, sheep) and less common (e.g., “Marder”, marten) animals (see Appendix A). Except for the embedded animal name, word lists with an animal were indistinguishable from lists used in regular trials. They followed the same design principles, contained the same preview manipulations in the same proportion as regular trials, and were presented randomly intermixed with them.

Procedure

After providing written informed consent, participants were seated in a dimly-lit, electrically shielded chamber at a distance of 60 cm from a CRT monitor (22 inch Iiyama VisionMaster Pro 514, resolution: 1024x768 pixels, vertical refresh rate: 160 Hz). The

screen was surrounded by a grey cardboard mask, which homogenized the peripheral visual field. In a 15-min block before the experiment proper, the EEG was recorded while participants performed calibration EMs that were later used for ocular artifact correction. Afterwards, participants received instructions that they would read lists of words and should indicate after each trial whether or not the list had contained the name of an animal. Participants were also told that words sometimes occurred twice in a list (in POF trials with identical preview) but that this was irrelevant for the task.

Figure 4.1

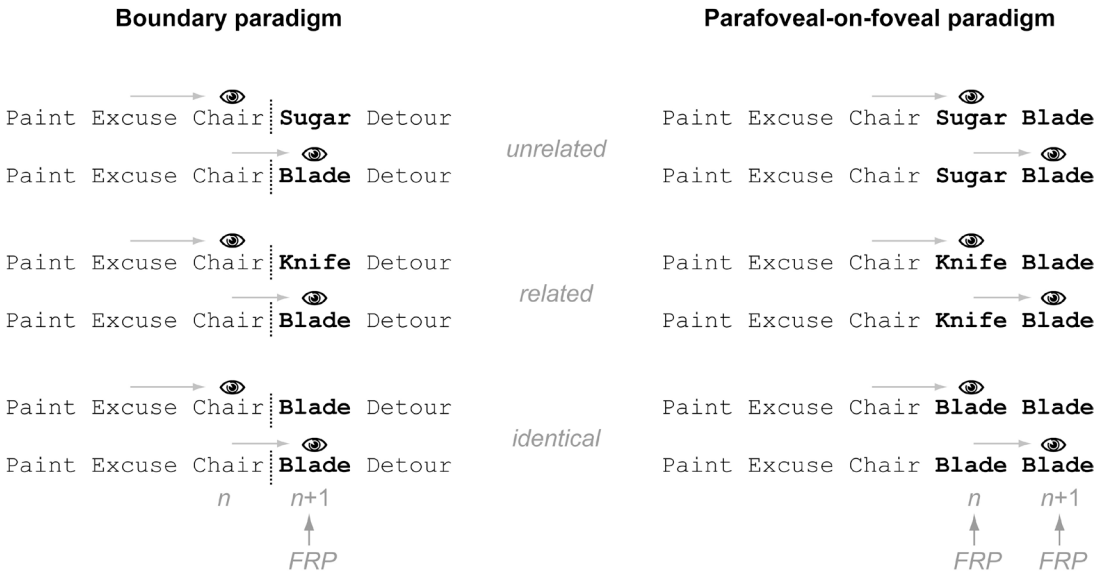


Illustration of paradigms used. Subjects read lists of nouns silently from left to right. Preview was manipulated for one noun, embedded at varying list positions. *Left panel*: In boundary trials, preview was manipulated with a saccade-contingent display change. While participants looked at pre-boundary word *n* (here: *chair*), the parafoveal preview for word *n*+1 was unrelated (*sugar*), related (*knife*), or identical (*blade*) to the later target word. During the saccade from *n* to *n*+1, upon crossing an invisible boundary (dashed line), the preview was exchanged to the target (*blade*). Right panel: In *parafoveal-on-foveal* trials, preview and target were simply shown at neighboring list positions. Again, the two words were unrelated (sugar-blade), related (knife-blade), or identical (blade-blade). Labels "FRP" mark fixations used as EEG time-locking points. In the actual experiments, critical words were not highlighted in bold and German nouns were used (here: *Messer/Klinge/Zucker/Bonbon*).

The trial scheme is illustrated in Figure 4.2A. Trials began with the presentation of a small black point on the left side of the screen. After a fixation on this point was registered, a list of five words appeared on the horizontal midline, together with a second small fixation point on the right side of the screen. Words were separated by one character space and presented in a black monospaced font (Courier) on a white background. One character

extended 0.43° horizontally. As required by German orthography, the first letter of each noun was capitalized. From the left fixation point, the distance to the left edge of word one in the list was 3.1° and at least 5.1° to the left edge of word two. The visual angles between the center of word *n* and the left edge of word *n*+1 varied between 1.29° and 1.94° (depending on the length of word n) with an average of 1.51° (*SD* = 0.18) in boundary trials and 1.56° (*SD* = 0.29) in POF trials.

In boundary trials, the invisible boundary was located in the middle of the space between word *n* and *n*+1. The average delay between the gaze crossing the boundary and stimulus replacement was 9.7 ms (= 3.5 ms computation time + 3.2 to 9.4 ms [0.5 to 1.5 display cycles] needed for the cathode ray to return to the screen center); this delay was shorter than the duration of the boundary-crossing saccade (*M* = 25.1 ms, *SD* = 6.5). The technical protocol was the same in the identical condition; here, the preview string was exchanged against itself.

Following list onset, participants read the five words, moving their eyes freely over the text. After finishing reading, they looked at the right fixation point. After 500 ms of fixation on this point, a screen appeared which prompted "Animal present? (Y/N)" and participants used two buttons to respond with left or right index fingers.

Participants read six lists for practice and 372 lists during the experiment. Sixty of these 372 lists (16.1%) contained an animal name and were excluded from data analysis. The remaining 312 lists were analyzed according to the design *preview* (identical, related, unrelated) × *paradigm* (boundary, POF), yielding 52 trials per condition.

Display change awareness was assessed in a structured interview after the experiment. Participants were first asked whether they had noticed "anything strange about the visual display of the text" (White et al., 2005). If they answered "no", they were informed that changes had taken place and asked again whether they had noticed any. If they did, participants were asked to (1) estimate the number of changes perceived, (2) report the identity of some of the preview strings, and (3) report the list positions at which changes had taken place.

EM recording

EMs were recorded binocularly with a video-based eye tracker (IView-X Hi-Speed 1250, SMI GmbH, Germany) at a rate of 500 Hz and an instrument spatial resolution of 0.01°. Head position was stabilized via the chin and forehead rests of the tracker. Tracking quality was controlled with a fixation check at the onset of each trial: After trial onset, if eye

position deviated more than 0.5° from the left fixation point or if binocular disparity exceeded ±0.5°, the tracker was recalibrated with a 9-point grid. Calibrations were performed whenever a check failed, but at least after every 30 trials.

EEG recording

The EEG was recorded from 42 Ag/AgCl scalp electrodes and four electro-oculogram (EOG) electrodes placed at standard 10-10 positions and referenced against the left mastoid. EEG electrodes were placed in a textile cap. EOG electrodes were positioned on the infraorbital ridge and outer canthus of each eye. An additional ground electrode was placed at FCz. Signals were amplified with BrainProducts DC amplifiers at a band pass from DC to 100 Hz and sampled at 500 Hz. Impedances were kept below 5 kΩ. Eye track and EEG were synchronized via shared TTL trigger pulses sent from the presentation PC (running Presentation, Neurobehavioral Systems Inc., Albany, CA) to both recording computers. Offline, the EEG was band-pass filtered from 0.2-40 Hz and re-referenced against the mean of all electrodes (average reference).

Fixation detection

Trials with blinks, missing data in the eye track, or incorrect manual responses were discarded. In the 96% remaining trials, saccades were detected with the binocular algorithm described in Engbert and Mergenthaler (2006; velocity threshold: 5 *SD*). Small saccades were considered part of a fixation if they spanned less than one character. Position data of the right eye was used to assign fixation locations, but left eye data was used for binocular validation. Fixations on inter-word spaces were assigned to the word to the right.

A total of n = 77,392 first-pass reading fixations (that is, excluding fixations following regressive saccades) were detected for all participants. In line with previous studies (Kliegl, Nuthmann, & Engbert, 2006), we removed extremely short (< 50 ms, n = 108) or long (> 1000 ms, n = 197) fixations and those for which the corresponding EEG segment contained non-ocular artifacts (n = 1,918, see below). Only trials were analyzed in which word n received a binocular fixation. This criterion excludes trials where word n was skipped and preview effects are unlikely. In *boundary* trials, only trials were considered in which (1) the display refreshed during the saccade (while visual thresholds are elevated due to retinal blurring and saccadic suppression; Ishida & Ikeda, 1989; Matin, 1974) and (2) both eyes crossed the boundary within 10 ms of each other. Rejected early changes usually occurred because the last pre-boundary saccade landed close to the boundary and

saccadic overshoot or system noise triggered the change prematurely. Late changes were usually (in 95% of cases) executed within 10 ms after saccade offset, but were rejected anyway. The same criteria were also applied to the identical preview condition. After the exclusion of all bad trials (due to blinks, missing eye tracking data, non-ocular EEG artifacts, skipped words, incorrect responses, or mistimed display changes), 88% of POF trials (M = 45.5 trials per participant and preview condition) and 67% of boundary trials (M = 34.7 trials) entered final data analysis.

EM analysis

First-pass fixation behavior was analyzed with three dependent variables: first fixation duration (FFD), single fixation duration (SFD), and gaze duration (GD). FFD is the duration of the first fixation on a word, irrespective of whether the word is subsequently refixated. SFD is fixation duration in case that a word only receives one first-pass fixation. GD is FFD plus the duration of all immediate refixations. One participant had no single-fixation cases in some cells of the design; SFDs are therefore reported for 34 participants in boundary trials.

Ocular artifact correction

Reading saccades introduce two types of EEG artifacts: Large corneoretinal artifacts from rotation of the bulbi (Brunia et al., 1989) and a brief myogenic spike potential at saccade onset (Keren, Yuval-Greenberg, & Deouell, 2010). To correct for corneoretinal artifacts, we applied the surrogate variant of Multiple Source Eye Correction (MSEC, Berg & Scherg, 1994; Ille, Berg, & Scherg, 2002), which performs well on natural reading data (Dimigen et al., 2011). Like principal component or independent component analysis (PCA/ICA), MSEC is a spatial filter (Ille et al., 2002) that models the recorded EEG as a linear combination of multiple scalp topographies (or components) that define the spatial layouts of artifact and brain activity. With surrogate MSEC, artifact topographies for each participant are empirically defined by averaging calibration EMs. Activity time courses for these artifact topographies are then estimated in the presence of a "surrogate" dipole model of brain activity (which defines a generic set of brain topographies), thereby reducing the accidental subtraction of genuine brain activity. As surrogate brain model we used BESA model "*BR_Brain Regions_LR.bsa*" without the most frontal regional source (regularization constant: artifact 0%, brain: 2%). Other procedural details were the same as in Dimigen et al. (2011).

Fixation-related potentials

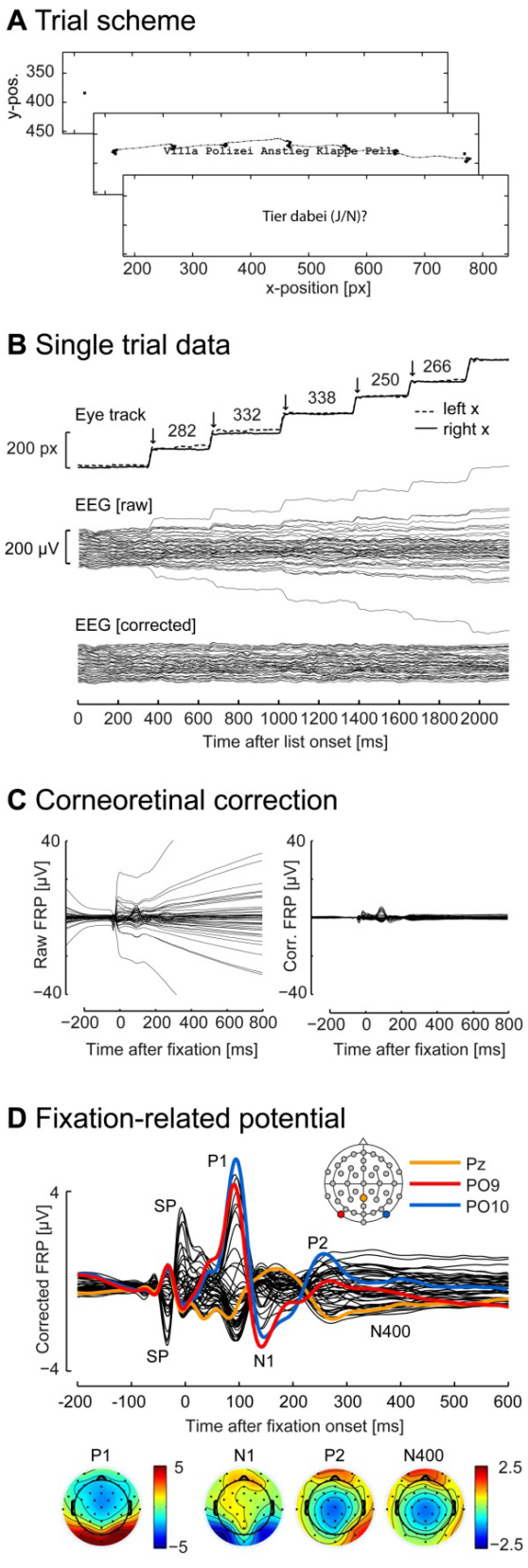
Segments of 1600 ms of artifact-corrected EEG were cut around each fixation onset (–600 to +1000 ms) and baseline-corrected by subtracting a 100 ms pre-fixation baseline. To exclude non-ocular artifacts (drifts or high-amplitude EMG), segments with a peak-to-peak voltage difference >120 μV in any channel were rejected (2% of segments). Remaining segments were averaged to obtain FRPs.

To compute FRPs aligned to word *n* (rather than *n*+1), we included only trials in which GD on *n* exceeded 240 ms and restricted the statistical analysis to the interval between 0 and 240 ms after fixation onset. This selection (cf. Baccino & Manunta, 2005; Simola et al., 2009) guarantees that readers are not already looking at word *n*+1 during the analysis interval, which would yield trivial positive results. The value of 240 ms was short enough to admit data contributions by all readers to all cells of the design and long enough to include the time range for which Baccino and Manunta reported a POF effect of semantic association (215 ms). For behavioral analyses on word n, all fixations were included.

Statistics

All results were collapsed across the two possible word positions in the list. EM measures were subjected to ANOVAs on the factor *preview*, separately for boundary and POF trials. Degrees of freedom were adjusted by multiplication with Huynh–Feldt's epsilon. We report the original *df*s, the Huynh-Feldt adjusted *p*-values, and effect sizes as partial eta squared (η_p^2). For FRP statistics, repeated measures ANOVAs on factors preview (3) × electrode (46) were conducted on mean FRP amplitude in consecutive 40 ms windows between 0 and 600 ms after fixation onset. In these ANOVAs, preview effects are only meaningful in interaction with electrode because the average reference sets the mean across electrodes to zero. To correct for multiple comparisons across time windows, these *p*-values were further corrected (p_{corr}) by applying the false discovery rate procedure by Benjamini and Hochberg (1995) as implemented by Groppe et al. (2011). Post-hoc contrasts between preview levels were computed for windows with a significant interaction.

Figure 4.2



A. Trial scheme. Following a fixation check on a point on the left, the list appeared and participants read it at their own pace. Gaze position of the right eye is plotted for this trial. After participants finished reading, they were asked whether one of the words was an animal. **B**. Synchronized horizontal eye track, raw EEG, and MSEC-corrected EEG for the trial shown above. Arrows mark fixation onsets, numbers indicate fixation durations (in ms). **C**. Grand-mean fixation-related potential (FRP), averaged across all fixations, conditions, and participants. All EEG channels are plotted superimposed and shown before (left) and after (right) MSEC. **D**. Detailed view of the artifact-corrected FRP. Scalp topographies are shown for the peaks of the P1, N1, P2, and for the N400 range (300-400 ms). The biphasic potential before fixation onset is the muscle spike potential (SP).

Results

Animal task

Participants responded correctly to the animal question after 97% of the trials (range: 92-99%). For lists with an animal, the mean false alarm rate (reporting an animal although none was present) was 1% and the miss rate (not recognizing the animal) was 16%. The rather high miss rate was likely due to the inclusion of some low frequency animals. For example, the animal with the worst detection rate, "Wisent" (European bison), was missed by 21 participants, indicating that it was unfamiliar to most participants.

Display change awareness

Of 35 participants, 11 remained completely unaware that the display was manipulated. These "unaware" participants did not recall seeing anything unusual about the display, even when they were informed about the changes after the experiment. The remaining 24 participants were conservatively labeled as "partially aware". Of these, 16 never realized that words were exchanged, but noticed for example a faint flicker on the screen once. Three of the partially aware participants had realized that words had been exchanged and reported that they had been able to determine the identity of a preview string at least once. The remaining five participants had realized that some previews were semantically related words. On average, the 24 partially aware participants estimated that they noticed 3.9 changes (min.: 1, max.: 10), or 2.7% of all visible changes. These instances were likely due to trials with badly timed changes that were excluded from analyses. Only four participants were able to correctly report the two list positions at which changes could occur during the experiment.

EMs in list reading

Participants read the list for an average of 2.3 s before looking at the right fixation point. First fixations, single fixations, and gaze durations lasted on average 298, 321, and 378 ms, respectively. Reading times increased moderately from the first (SFD: M = 299 ms) to the penultimate (SFD: M = 338 ms) word in the list. As in sentence reading, words were typically fixated slightly left to their center. Most saccades were oriented rightward but there were some (3%) regressions towards earlier words in the list, and 36% of words received one or more refixations. The mean amplitude of inter-word saccades was 2.7° (6.3 characters). Incoming saccade amplitudes did not differ between preview conditions in

boundary or POF trials. This is important, because saccade amplitude modulates the neural response after saccade offset (Dimigen, Valsecchi, Sommer, & Kliegl, 2009).

Quality of corneoretinal correction

Visual inspection of the continuous EEG and of averaged FRPs before and after correction suggested that MSEC eliminated corneoretinal artifacts almost entirely (Figure 4.2B and 4.2C). Correction quality was similar to that previously obtained for sentence reading (Dimigen et al., 2011). As an objective criterion to test correction quality, we correlated each EEG channel with the (electrically independent) horizontal eye position from the eye tracker before and after MSEC, following the procedure in Dimigen et al. (2011). After correction, all correlation coefficients were $|r| < 0.09$ and the mean of all $|r|$ was 0.03, indicating that artifacts correction worked well. In contrast, MSEC does not remove the brief muscle spike potential at saccade onset but this is not a serious problem for EEG analyses in the time domain (if saccade properties do not differ between conditions).

Table 4.2. Reading times on post-boundary word n+1 in boundary trials

	Reading times on word *n*+1		
	Identical Preview	Related Preview	Unrelated Preview
First fixations (ms)	303 (25)	316 (27)	317 (26)
Single fixations (ms)	325 (29)	347 (38)	345 (33)
Gaze duration (ms)	350 (28)	370 (33)	365 (33)

Note. Given are mean and SEM.

Boundary trials

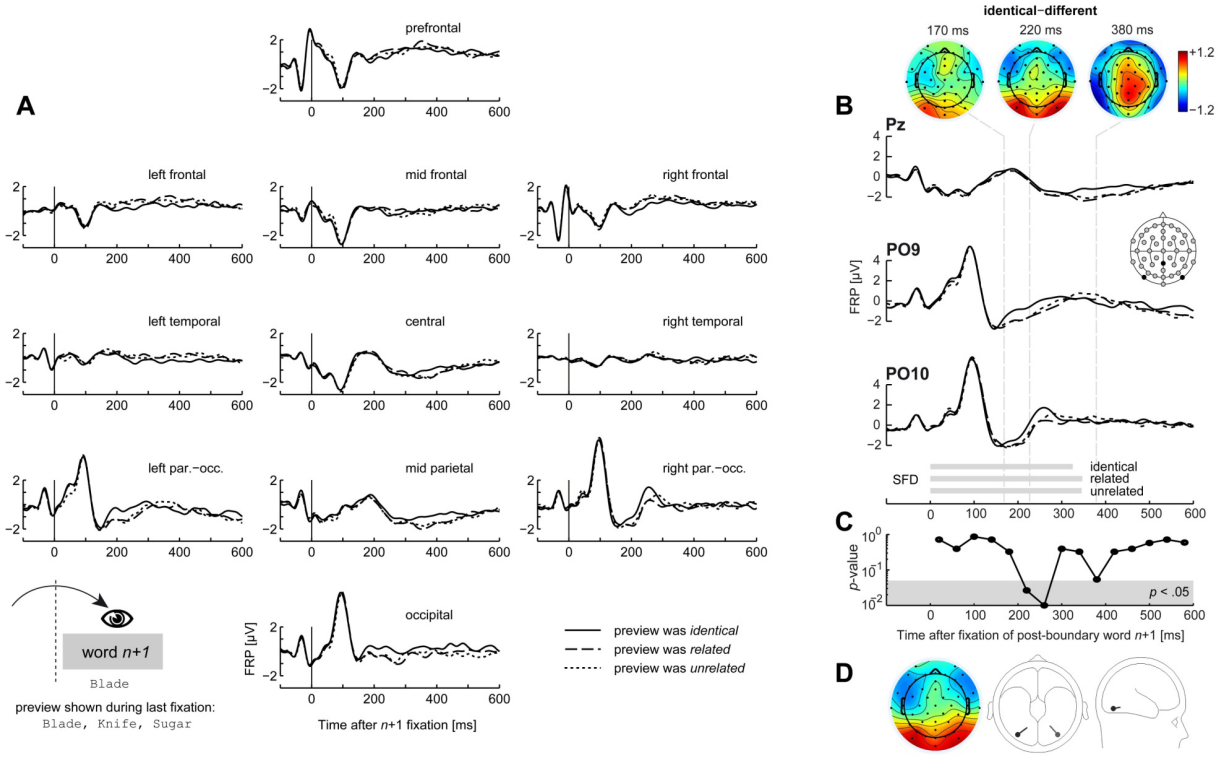
EMs

Table 4.2 shows reading times on the post-boundary word *n*+1 as a function of the preview available during the previous fixation of the pre-boundary word *n*. A main effect of preview condition was found for all reading time measures: first fixation duration, $F(2,68) = 5.4$, $p = 0.007$, $\eta_p^2 = .014$, single fixation duration, $F(2,66) = 5.9$, $p = 0.006$, $\eta_p^2 = 0.15$, $\varepsilon = 0.92$, and gaze duration, $F(2,68) = 5.1$, $p = 0.009$, $\eta_p^2 = 0.13$. Post-hoc comparisons showed that all three measures were shorter after identical previews, both compared to semantically related (all ts > 2.5, all ps < 0.02) and unrelated previews (all ts > 2.4, all ps < 0.03). This result replicates the classic identity preview benefit established in many eye tracking studies. The size of this benefit (unrelated minus identical) was 14 ms in FFD ($p = 0.003$), 20 ms in SFD ($p = 0.002$), and 15 ms in GD ($p = 0.025$). In contrast, there was no difference

between related and unrelated previews in any measure (all *t*s < 1, all *p*s > 0.38). Behavior therefore provided no evidence for a benefit from semantically related previews.

As a control, we also analyzed reading times on the filler that served as pre-boundary word *n*. Please note that in the boundary paradigm, the filler at position *n* and the preview word shown for word *n*+1 are always unrelated words. Therefore, as expected, fixation times on *n* did not differ between preview conditions (all *F*s < 1, all *p*s > 0.50).

Figure 4.3



Results from boundary trials. **A.** Grand-average FRPs, time-locked to first fixations on post-boundary word *n*+1. Please note that at time 0, the same word is fixated in all conditions: Conditions only differ in terms of the preview that was available during the *previous* fixation. Electrodes are clustered as follows: Occipital (O1, Oz, O2, Iz), left parieto-occipital (P7, PO7, PO9), right parieto-occipital (P8, PO8, PO10), mid-parietal (P3, Pz, P4, POz), central (FC1, FC2, Cz, Cp1, Cp2), left central-temporal (FC5, C3, CP5, T7, A1), right central-temporal (FC6, C4, CP6, T8, A2), frontal (F3, Fz, F4, AFz), left frontal (AF7, F7, FT9), right frontal (AF8, F8, FT10), and prefrontal (Fp1, Fpz, Fp2). **B.** FRP at parietal (Pz) and left (PO9) and right (PO10) occipitotemporal electrodes. Topographies show the difference between identical minus different (related or unrelated) previews at 170 and 220 ms (*preview positivity*, PP) and at 360 ms (late N400-like trend). Grey bars show single fixation durations (SFD). **C.** *p*-values for the *preview* × *electrode* interaction. **D.** Effect topography and dipole model of the PP (interval 200-280 ms) suggested bilateral generators in extrastriate or occipitotemporal cortex.

FRPs

Figure 4.3 shows the corresponding grand-average FRPs, time-locked to the first fixation on word *n*+1. The absolute FRP wave shapes were characterized by the biphasic muscle spike potential around time zero (Keren et al., 2010), followed by a dominant occipital P1-N1 complex. This complex consisted of the positive-polarity lambda response (the P1-equivalent in FRPs) peaking 96 ms after fixation at right occipitotemporal electrode PO10, and a negative peak around 140 ms resembling the N1 (or N170) component in stimulus-locked ERPs. The P1 was considerably larger over the right (5.74 μV at PO10) than the left hemisphere (4.61 μV at PO9) during fluent reading, $t(34) = 2.87$, $p < 0.01$. Conversely, the following N1 peak was larger over the left (-2.63 μV) than right (-2.20 μV) hemisphere, but this difference did not reach significance (Figure 4.2D).

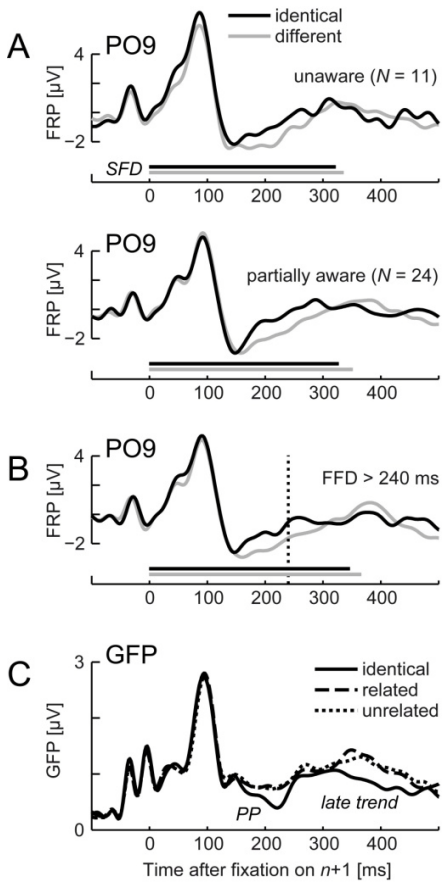
Importantly, FRPs aligned to word *n*+1 differed as a function of the preview that had been available during the fixation of *n*. As Figure 4.3 shows, wave shapes in the three conditions were similar until about 170 ms after fixation onset. However, after the N1 peak, the FRP in the identity preview condition began to diverge from that observed after related or unrelated previews. This effect started at left occipitotemporal electrode PO9 (Figure 4.3B), spread shortly afterwards also to right-hemisphere electrode PO10, and reached a maximum size at both electrodes at 252 ms. Statistical testing in 40 ms windows onset yielded a significant *preview* × *electrode* interaction between 200 to 240 ms, $F(90,3060) = 2.7$, $p_{corr} < 0.026$,$\eta_p^2 = 0.07$, and between 240 to 280 ms after fixation onset, $F(90,3060) = 3.5$, $p_{corr} < 0.01$,$\eta_p^2 = 0.09$ (Figure 4.3C). Post-hoc contrasts showed that in both intervals, the identical condition differed significantly from both the related and the unrelated condition. Thus, a correct parafoveal preview during the previous fixation led to a modulation of FRP amplitude over occipitotemporal areas, beginning after the N1 peak, reaching a maximum around 250 ms, and lasting until approximately 280 ms. In the following, we will refer to this decreased negativity to previewed words as the *preview positivity (PP).*

Visual inspection also suggested a possible late effect of preview that was spatially and temporally distinct from the earlier PP. Figure 4.3B shows that from about 320 to 500 ms, during the traditional N400 time window, voltages at mid-parietal electrodes were more positive after identity previews. Between 360 and 400 ms, this difference was marginally significant, $F(90,3060) = 2.4$, $p_{corr} = 0.05$, $\eta_p^2 = 0.07$ (Figure 4.3C).

In contrast, we observed no benefit from semantically related previews in FRPs: Amplitudes did not differ significantly after related and unrelated previews in any time window.

As a control, FRPs were time-locked to fixations on the pre-boundary word *n*. As expected, preview condition had no effect on FRPs evoked by this fixation.

Figure 4.4



Control analyses for boundary trials. **A.** Preview benefit as a function of display change awareness. Mean single fixation durations (SFD) are plotted as horizontal bars. **B.** Preview benefit in a subset of target fixations lasting longer than 240 ms. **C.** Preview benefit in the EEG's global field power (GFP).

Source estimation

In an exploratory analysis we modeled the generators of the PP with equivalent current dipoles in BESA (Brain Electromagnetic Source Analysis, v5.2, Megis). Based on the dipolar PP topography evident in Figure 4.3D, a dipole pair with a bilateral symmetry constraint was fitted to the mean effect in the grand-average FRP between 200-280 ms using the contrast *identical* minus *different* (related and unrelated condition collapsed). As Figure

4.3D shows, the solution was compatible with bilateral sources in extrastriate occipital or occipitotemporal cortex (approx. Talairach coordinates: x = ±36, y = -76, z = -12). However, the model was not entirely satisfactory in terms of residual variance (5.4% at best time point) and can only be treated as an approximation of the underlying source configuration.

Control analyses

The results presented so far suggest that the preview positivity in FRPs reflects a processing advantage from parafoveal information obtained during the previous fixation. Four alternative explanations were also tested.

First, the effect might be related to the conscious perception of the display change on a few occasions. This explanation seems unlikely, since trials with badly timed changes were excluded. Nevertheless, this hypothesis was tested by comparing results of partially aware and completely unaware participants. Figure 4.4A shows that identity benefits were significant in both groups, irrespective of awareness. For partially aware participants, the benefit (identical minus unrelated) was 19 ms in SFDs, $t(22) = 2.5$, $p = 0.02$, and -0.98 μV in FRP amplitude (measured at PO9 between 200 and 280 ms; $t(22) = 3.5$, $p = 0.002$). For unaware participants, the benefit was 22 ms in SFDs, $t(10) = 2.3$, $p = 0.04$, and -0.76 μV in FRPs, $t(10) = 2.5$, $p = 0.03$.

Second, we tested whether the effect is a trivial reflection of the oculomotor effect. A serious methodological challenge for FRP recordings during free viewing is temporal overlap between brain potentials evoked by successive fixations. If fixations are shorter in one experimental condition, potentials evoked by the next fixation will overlap at an earlier latency, compared to conditions with longer fixations. This can produce artificial FRP differences that are merely a reflection of the behavioral effect. To exclude this possibility, we reanalyzed the FRP and included only cases in which the first fixation on n+1 lasted more than 240 ms (68% of cases). In this average, shown in Figure 4.4B, the interval up to 240 ms is free of overlapping potentials from the next fixation. The preview effect was still observed, ruling out this possibility.

Third, the PP modulation might reflect a visually evoked potential (VEP) elicited by the peri-saccadic display change. In the identical condition, the word was exchanged against itself; meaning that there was no visible transient on the screen. Thus, the effect could be part of an additional P1-N1 complex evoked by the change in the other conditions. Importantly, the five ANOVA windows before 200 ms yielded no significant effect of preview. Nevertheless, we scrutinized the early FRP intervals for signs of a VEP in the related and the unrelated condition. As the display refreshed M = 16 ms before fixation

onset, a P1-like VEP should be observed at occipital electrodes about 90-140 ms later (i.e., around 74-124 ms). No indication of an early VEP was observed (Figure 4.3). Similarly, as Figure 4.4C shows, there was no sign of early differences in the EEG's global field power (Murray, Brunet, & Michel, 2008). It therefore seems unlikely that the preview positivity (a relative negativity in conditions with dissimilar preview) is an artifact of the peri-saccadic transient.

Fourth, the effect might be related to residual corneoretinal artifacts. This can be ruled out on several grounds: (1) MSEC removed most of the corneoretinal artifacts. (2) The effect was found at deep posterior electrodes that receive only a small fraction of the artifact. In particular, the effect was also found at electrode Oz. Due to its posterior midline position, this electrode was uncorrelated to eye position even in the uncorrected EEG (r = 0.006, p = 0.74). (3) The effect was replicated for fixations lasting longer than 240 ms. For these fixations, the interval from 0 to 240 ms (see dashed line in Figure 4.4B) is by definition free of EM artifacts.

Table 4.3. Reading times in parafoveal-on-foveal trials as a function of the relationship between word n and n+1

	Reading time on word *n*			Reading time on word *n*+1		
	Identical	Related	Unrelated	Identical	Related	Unrelated
First fixations (ms)	277 (18)	292 (22)	297 (23)	265 (22)	291 (23)	301 (23)
Single fixations (ms)	293 (20)	312 (26)	315 (25)	275 (27)	309 (29)	327 (30)
Gaze durations (ms)	319 (23)	342 (29)	345 (29)	299 (28)	335 (29)	355 (34)

Note. Given are mean and SEM.

Parafoveal-on-foveal trials

In POF trials, preview and target were simply shown at adjacent list positions. This alternative paradigm allows us to test whether properties of the second word *n*+1 exert an influence on behavior or EEG while the eyes still rest on the previous word *n*. At the same time, these trials served as a control for our word materials: Even without any parafoveal preprocessing, we should see robust effects of repetition priming (in case of two identical words) and semantic priming (in case of two related words) once the reader looks directly at word *n*+1.

EMs on word n

The left part of Table 4.3 shows reading times on word *n* as a function of whether word *n*+1 was identical, related, or unrelated. All EM measures were influenced by the type of word shown parafoveally, as evident in main effects of preview condition on FFD, $F(2,68) = 14.2$, $p < 0.001$, $\eta_p^2 = 0.30$, $\varepsilon = 0.95$, SFD, $F(2,68) = 13.0$, $p < 0.001$, $\eta_p^2 = 0.28$, and GD, $F(2,68) = 12.5$, $p < 0.001$, $\eta_p^2 = 0.27$, $\varepsilon = 0.91$. In each case, the effect was due to the identical preview condition. Reading times on *n* were significantly shorter when *n*+1 was identical, both relative to the related (all $t(34) > 3.8$, all $ps < 0.002$) and the unrelated condition (all $ts(34) > 4.1$, all $ps < 0.001$). In contrast, reading times were not influenced by whether *n*+1 was related or unrelated; FFD: $t(34) = 1.5$, $p = 0.156$; SFD: $t(34) = 0.8$, $p = 0.441$; GD: $t(34) = 0.6$, $p = 0.549$.

FRPs locked to word n

Figure 4.5 show the corresponding FRPs. The left sides of the time axes in figure 5A and 5B shows the FRP for the first fixation of word *n*. Importantly, the type of word shown at *n*+1 had no effect on FRPs time-locked to *n*. Not only was there no semantic effect, there was also no difference between the unrelated and the identical condition. Whereas fixation times on *n* were significantly shorter when the parafoveal word was identical to the fixated word, FRPs did not reflect this parafoveal-on-foveal effect.

EMs on word n+1

Once word n+1 was directly fixated, the relationship between n and n+1 clearly influenced reading behavior (Table 4.3, right side). All three EM measures showed identity priming and semantic priming, as suggested by highly significant main effects of preview condition on FFD, $F(2,68) = 31.9$, $p < 0.001$, $\eta p2 = 0.48$, $\varepsilon = 0.89$, on SFD, $F(2,68) = 43.2$, $p < 0.001$, $\eta p2 = 0.56$, $\varepsilon = 0.83$, and on GD, $F(2,68) = 42.1$, $p < 0.001$, $\eta p2 = 0.55$, $\varepsilon = 0.77$. Post-hoc contrasts revealed that reading times were shorter when both words were identical, as compared to when they were merely related ($ts > 5.2$ and $ps < 0.001$ in all three measures), and shorter when the words were related as compared to when they were unrelated (all $ts > 2.9$, all $ps < 0.01$). Size of the semantic effect was 10 ms in FFD ($p < 0.01$), 18 ms in SFD ($p < 0.001$), and 20 ms in GD ($p < 0.001$).

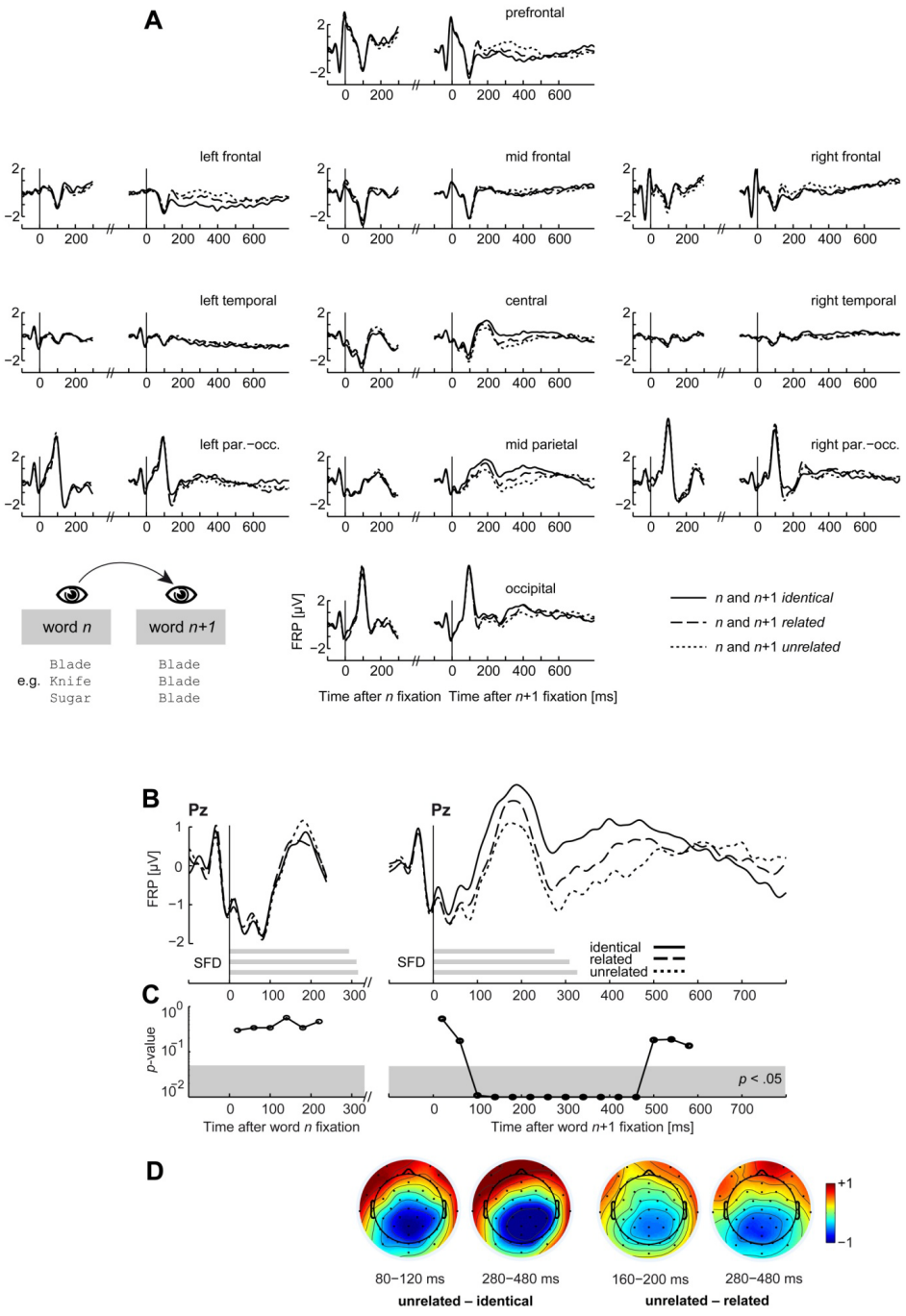
FRPs locked to word n+1

Clear priming effects were also observed in FRPs time-locked to fixating word *n*+1 (right sides of time axes in Figure 4.5A and 4.5B). Results replicated the well-established pattern from foveal priming studies (Rugg, 1985): The N400 component was most negative for

unrelated, intermediate for related, and most positive for repeated words and its classic centroparietal scalp distribution was similar for both types of priming (this also suggests that the effect in the identical condition was not an oddball P300 to the unusual word repetition). These results confirm that the word pairs were capable of producing robust priming effects in foveal vision.

Importantly, N400 effects arose at very short latencies after fixation onset. Despite correction for multiple comparisons, window-wise ANOVAs yielded a significant *preview* × *electrode* interaction starting at 80 ms and lasting until 480 ms after fixation onset (all $F(90,3060) > 2.6$, all $p_{corr} < 0.05$; all $\eta_p^2 > 0.07$; maximum F-value of 8.7 between 320-360 ms with $p_{corr} < 10^{-6}$ and $\eta_p^2 = 0.20$). The contrast identical versus unrelated reached significance between 80-120 ms ($p = 0.003$) and remained significant until 480 ms; the contrast related versus unrelated reached significance between 160-200 ms ($p = 0.012$) and also remained significant until 480 ms. Note that these N400 onset latencies are much shorter than those typically seen in experiments with foveal repetition priming or semantic priming (e.g., Rugg, 1987).

Figure 4.5



Results from parafoveal-on-foveal trials. **A.** Within each plot, FRPs are shown time-locked to the first fixation on word *n* (left part of time axis) and for the subsequent fixation on word *n*+1 (right part of time axis). **B.** Detailed plot for midparietal electrode Pz. Mean single fixation durations (SFD) in the three conditions are plotted as horizontal bars. **C.** *p*-values for the *preview* × *electrode* interaction. The relationship between word *n* and *n*+1 did not influence FRPs aligned to of word *n*. However, shortly after word *n*+1 was looked at, N400 priming effects arose at centroparietal electrodes. **D.** Scalp distribution of effects, aligned to fixations on word *n*+1, are shown for the first significant time window and for the N400 time range.

Discussion

Extrafoveal preprocessing of soon-to-be fixated items is a property of natural vision that is rarely considered in EEG studies on visual perception. For the case of reading, a large body of eye-tracking studies has shown that readers spend less time on parafoveally previewed words. In a list reading design, we investigated the impact of this trans-saccadic preview benefit on EEG correlates of word recognition and tested which types of information contribute to this facilitation. Effects were analyzed simultaneously in fixation behavior and fixation-triggered potentials (FRPs) and with two complementary experimental approaches: as preview benefits in boundary trials and as parafoveal-on-foveal (POF) effects.

Results replicate several common observations in oculomotor behavior. In particular, in boundary trials we demonstrated an identity preview benefit but no semantic preview benefit. A key novel finding was a *preview positivity* (PP) – a marked difference in FRP morphology when a correct preview on the fixated word had been available during the preceding fixation. On the other hand, a semantic preview effect was not present in FRPs either. Similarly, parafoveal-on-foveal trials without display changes did not reveal a POF influence of semantic information on EM measures or FRPs time-locked to the first word of the critical word pair. However, N400 effects from identity priming and semantic priming emerged very shortly (around 80 and 160 ms, respectively) after the second word was directly fixated. Like the PP effect, this result suggests that time course and wave shape of EEG correlates of word recognition are different during fluent reading because words are already partially processed once they enter foveal vision. The following discussion will be organized according to the main questions of the present study: whether there is a neural signature of preview benefits and whether this benefit extends to semantic information gleaned from the parafovea.

A neural correlate of the preview benefit?

With an effect size of 20 ms in single fixations, the identity preview benefit in boundary trials was within the range usually observed in sentence reading. What is the neural basis of this classic behavioral facilitation? Based on findings that preview benefit is at least partially robust against trans-saccadic changes in spatial location and in low-level visual features (McConkie & Zola, 1984; Rayner et al., 1980) we hypothesized that EEG effects of identity previews would not manifest on the earliest stages of vision, but possibly in ventral-stream systems linked to orthographic processing.

The overall FRP waveshape resembled that of visual ERPs in many aspects and was also characterized by a P1-N1 complex. In line with a previous report (Dimigen et al., 2011), the visual P1 after fixation was considerably larger over the right hemisphere. However, this asymmetry reversed for the following N1 which was numerically larger over the left hemisphere. The result is reminiscent of the well-established left-hemispheric asymmetry of the N170 component to orthographic stimuli (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999), indicating that this finding generalizes to fluent reading.

In line with our hypotheses, preview had no significant effect on early FRP intervals, including the P1. However, shortly after the N1 peak, around 170 ms, a difference emerged between the condition with identity preview and the two conditions with related or unrelated previews. This preview positivity consisted in a decreased negativity over low occipitotemporal sites in the identical condition that started over left occipitotemporal electrodes but was soon followed at right-hemisphere electrodes. The activation pattern reached significance between 200 and 280 ms and was compatible with bilateral generators in occipitotemporal cortex.

Importantly, the PP was independent of display change awareness and not an artifact of overlapping brain activity or corneoretinal potentials. Furthermore, there was no indication that FRPs were influenced by visually-evoked potentials (VEPs) to the display change. A peri-saccadic visual transient might elicit a VEP not present in the identical preview condition in which the string was exchanged against itself. However, this explanation for the PP seems unlikely. Whereas sufficiently strong suprathreshold stimuli presented during saccades can elicited VEPs (Anagnostou, Kleiser, & Skrandies, 2000; Skrandies & Laschke, 1997) most studies found that responses to peri-saccadic stimuli are strongly decreased or absent (Chase & Kalil, 1972; Duffy & Lombroso, 1968; Gross, Vaughan, & Valenstein, 1967; Michael & Stark, 1967). This holds true in particular if the stimulation occurs shortly after saccade onset and its intensity is below conscious detection thresholds. In the present study, changes occurred during the saccade, were of low intensity, and not perceived by the subject (when properly timed). Second, a VEP should manifest at least as a P1-like occipital positivity in the two visually dissimilar conditions. In contrast, there were no significant effects of preview condition prior to 200 ms and the following PP effect was a relative negativity (rather than positivity) in conditions with a change.

What processes underlie the preview positivity? It is possible that the benefits from identity previews are compound effects that reflect facilitation at multiple levels (e.g., sub-letter visual features, orthographic representations, phonological and lexical representations).

However, the time range, topography, estimated sources, and left-hemisphere onset of the PP are at least compatible with the notion from EM research that much of the benefit results from a pre-activation of abstract orthographic codes (Rayner, 1998).

A common view in ERP research is that pre-lexical orthographic influences emerge in a time range between 150-200 ms while lexical influences begin 250 to 400 ms after word onset (Barber & Kutas, 2007; but see also Pulvermüller et al., 2009). The occipitotemporal N170 component is usually linked to early orthographic processing (e.g., Bentin et al., 1999; Maurer, Brandeis, McCandliss, 2005) and priming studies find case-independent orthographic priming around 250 ms (Carreiras, Perea, Vergara, & Pollatsek, 2009; Grainger et al., 2006; Holcomb & Grainger, 2006).

Interestingly, identity previews benefits in the current study – the PP and the N400-like trend - show similarities to the pattern of results established with foveal masked priming studies. When a masked repetition prime or partial orthographic prime is presented at short prime-target intervals (Holcomb & Grainer, 2007) a sequence of priming effects is observed: an early effect around 150 ms, called N/P150, a mid-latency effect from about 180 ms to 300 ms, called N250, and a late effect on N400. Only the latter two effects are robust against slight changes in the spatial location of prime and target (Dufau, Grainger, & Holcomb, 2008) as they would occur in a fluent reading situation. The N250, which is rather similar to the PP in terms of timing, has been interpreted as reflecting a mapping of abstract orthographic information to whole-word representations. Although N250 and PP differ in terms of scalp topography, these phenomena could be functionally related, a question that should be investigated in future research.

Unfortunately, little is known about neural effects of parafoveal priming. An exception is an MEG study by Pernet, Uusvuori, and Samelin (2007) who investigated parafoveal repetition priming in the lexical decision task. Primes presented in the right hemifield influenced the magnetic fields evoked by subsequently presented foveal targets beginning 160 ms after target onset in left occipitotemporal and superior temporal regions. While these results were not obtained during fluent reading, there are again similarities to the PP effect reported here.

In addition to the earlier PP, there was a trend for a late effect from identical previews that was temporally and topographically distinct. This pattern consisted of more positive centroparietal amplitudes after identity previews during the N400 time window between 360 and 400 ms. While the finding of the PP suggest that it is primarily EEG components in

a mid-latency range that are sensitive to preview, this trend provides an indication that identity previews can also influence the N400 and later stages of word processing.

Comparison to foveal repetition priming. The study design allows us to compare the effect of a correct parafoveal preview (in boundary trials) to the full-blown effect of trans-saccadic word repetitions (in POF trials). In POF trials with an identical preview, the same word was foveated on two subsequent fixations. When FRPs were aligned to the second word, and if this second word was a repetition of the first one (rather than unrelated to it), the FRP at centroparietal electrodes showed a strong positive deflection resembling the repetition priming effect on the N400 established in ERPs (Rugg, 1985). In these studies, the parietal positivity to repeated words is interpreted as a reduced negativity (i.e. N400) which is usually superimposed on a large positivity but now diminished due to repetition. Our results extend this literature by showing that N400 repetition effects also occur when the same string is fixated twice across an intervening saccade during fluent reading.[22]

If repeated fixations of the same word elicit a large N400 repetition effect, why was the effect of identity previews in boundary trials limited to the PP and a marginally significant trend in the N400 window? A likely explanation for this difference is that a directly fixated (and therefore fully processed) first word also primes lexico-semantic or post-lexical stages once the second word is fixated. In contrast, the PP and the N400 trend after (only partially processed) parafoveal previews would reflect a more pure correlate of unconscious orthographic or phonological priming.

Semantic processing of parafoveal words?

Our second goal was to test whether readers also extract word meaning parafoveally. In boundary trials, we tested whether related previews facilitate target processing. In the current list reading task, we found no evidence for such a semantic preview benefit in behavior or FRPs. In particular, there was neither a PP as seen for identity previews, nor a late N400-like effect.

In POF trials, we tested whether FRPs to word *n* are influenced by its semantic relatedness to the upcoming word *n*+1. Within the analysis interval of 240 ms, the FRP was not influenced by properties of the upcoming word, irrespective of whether it was unrelated, related, or identical. This result is at odds with results from Baccino and Manunta (2005)

22 This repetition effect is interesting because about 15% of all words during reading receive multiple fixations (Rayner, 1998). Refixations during reading may have a similar electrophysiological effect as seen here two fixations on an identical word.

who reported a POF effect of semantic association on a P2 component (around 215 ms). Such a semantic POF effect was not replicated by Simola and colleagues (2009); however, these authors modified the paradigm and had the parafoveal word appear to the left or right of the foveal word. In the current, more natural reading situation, we also found no semantic POF effect in the P2 window (or any other time window), which is consistent with the lack of a semantic preview benefit in boundary trials.

Latency of semantic access. When did readers retrieve word meaning in our list reading task? Parafoveal-on-foveal trials allow us to estimate an upper temporal limit for access to semantic codes. In line with classic ERP findings (Rugg, 1985), N400 amplitude to the second word was largest after unrelated, intermediate after related, and smallest (most positive) after identical first words. Importantly, the contrast between the related and unrelated conditions reached significance already 160 ms after the second word was fixated. This suggests that the meaning of both words was available no later than at this point in time. Compared to traditional foveal priming studies (e.g. Rugg, 1987) this is an unusually short latency for semantic effects. Together with the benefit observed in boundary trials, this temporal shift is most plausibly explained by assuming that the second word was already at least partially processed by the time it received a direct fixation, thereby leading to an earlier onset of semantic N400 effects. This conclusion is also in line with two recent FRP studies which have found that N400 word predictability effects tend to arise earlier under natural reading conditions with preview (Dimigen et al., 2011; Kretzschmar et al., 2009).

Finally, it should be noted that although people scan lists of words every day (e.g. shopping lists, inventories, email subject lines) this activity differs from sentence reading in several ways. Sentences not only allow context-based predictions about upcoming words, but also include short and highly frequent function words and these properties are known to increase the amount of parafoveal processing (Henderson & Ferreira, 1990; Kliegl et al., 2006). The existence of semantic preview effects in the EEG should be further investigated in the context of sentences.

Conclusions

Parafoveal processing must be considered if one wishes to draw conclusions about reading from studies of word recognition. Here we demonstrated that the wave shape and timing of EEG correlates of word recognition is different under normal reading conditions that allow preview. However, extrafoveal preprocessing is in no way exclusive to reading, but part of any real-world viewing situation. We therefore speculate that other mid-latency EEG

components, such as the N170 evoked by scanning scenes, objects, or faces, could be modulated by preview in similar ways as seen here for words. Our results document that saccade-contingent display manipulations can be combined with EEG recordings during free viewing, opening the door for systematic explorations of the impact of preview on neural correlates of visual perception.

Acknowledgements

We thank Benthe Kornrumpf, Susann Meyberg, Ulrich Reinacher, and Katharina Schäfer for help with data collection and creating preview-target pairs, Kay-Michael Würzner for computing collocation norms, Michael Dambacher for creating the pool of filler words, and Olaf Hauk for comments on an earlier manuscript version. This work was financed by DFG Research Group 868.

Supplementary Materials for Publication 4

Matching of pairs on non-semantic dimensions

Since related and unrelated word pairs comprised of the same words, lexical properties (such as word frequency) were matched for both types of pairs. Nevertheless, it is still possible that semantically related words are more similar to each other than unrelated words on a visual, orthographic, or phonological level. To rule out priming based on non-semantic properties, preview and target never started with the same letter or phoneme. In addition, related pairs were matched to unrelated pairs on 15 non-semantic measures of word similarity (summarized in Table 4.1 of Dimigen, Kliegl, & Sommer, 2012). For this matching, a simple resampling method was used. On each of 100,000 iterations, our algorithm randomly sampled 312 preview-target units (two related pairs plus their recombinations) from a total pool of 317 units that were considered suitable after the semantic rating. For each random sample of 312 units, it then computed a weighted sum of several measures of non-semantic word similarity, separately for related and the unrelated pairs. The best-matching solution was kept and used for the experiment.

Visual similarity

Visual similarity between targets and previews was measured by comparing letters located at corresponding positions in the two strings. As a first measure, we counted the letters that shared the same stroke direction. Stroke direction matches if both letters have an ascender (e.g., 'd' and 'f'), both have a descender (e.g., 'g' and 'j'), or both have neither ascender nor descender (e.g., 'a' and 'c'). As a second measure, we used empirical data on letter confusability. Confusability is the likelihood of confusing a letter with another letter after brief visual presentation. For upper-case letters, we used a confusability matrix by Bouma (1971; his Table 3). For lower-case letters, we used the matrix from Mueller and Weidemann (2008, their Table 3), after transforming the data to a format similar to that used by Bouma.

Orthographic similarity

Orthographic similarity was determined location-specific and location-invariant (i.e., irrespective of letter position). As a location-specific measure, we counted instances where the same letter occurred at the same position in both strings. This was summarized as the Hamming Distance (Hamming, 1950), which is the edit distance (Levenshtein Distance) for two strings of equal length. As a location-invariant measure, we counted the letter bigrams

and letter trigrams in the preview that also occurred somewhere in the target. Orthographic similarity based on bigrams was also operationalized as the Dice Coefficient (Dice, 1945) based on letter bigrams. The Dice coefficient was computed following Lambert et al (2002).

Phonological similarity

Phonological similarity was defined as the edit distance (Levensthein distance) based on phonemes (instead of letters). For this, all nouns were translated into the SAMPA phonetic alphabet. SAMPA codes were retrieved from the BOMP dictionary (Bonn machine-readable pronunciation dictionary; Portele, Krämer, and Stock, 1995). Some of the nouns (39 nouns) were not contained in the BOMP dictionary; for these cases, SAMPA codes were extracted from the *dlexDB* database (automatic phonemization).

List of prime-target word pairs and animal names used in Publication 4

Related and unrelated pairings are shown with the respective mean semantic rating score obtained in the pre-experiment.

Four letters (62)

1. Wind - Luft (4.73) / Blut (1.27)
2. Mord - Blut (4.53) / Luft (1.13)
3. Geld - Euro (4.87) / Säge (1.33)
4. Holz - Säge (4.47) / Euro (1.27)
5. Ober - Wirt (4.53) / Flut (1.40)
6. Ebbe - Flut (4.73) / Wirt (1.20)
7. Saum - Naht (4.53) / Brot (1.13)
8. Mehl - Brot (4.47) / Naht (1.27)
9. Tüte - Sack (4.67) / Ziel (1.20)
10. Plan - Ziel (4.47) / Sack (1.40)
11. Hall - Echo (4.73) / Grün (1.33)
12. Blau - Grün (4.47) / Echo (1.33)
13. Wall - Burg (4.40) / Bett (1.33)
14. Sofa - Bett (4.53) / Burg (1.13)
15. Berg - Höhe (4.60) / Zahn (1.20)
16. Arzt - Zahn (4.53) / Höhe (1.53)
17. Rose - Dorn (4.47) / Halt (1.53)
18. Stop - Halt (4.80) / Dorn (1.40)
19. Tuch - Hals (4.27) / Reis (1.67)
20. Korn - Reis (4.73) / Hals (1.13)
21. Kahn - Ufer (3.80) / Ehre (1.07)
22. Ruhm - Ehre (4.73) / Ufer (1.27)
23. Rohr - Ofen (4.27) / Meer (1.47)
24. Sand - Meer (4.73) / Ofen (1.40)
25. Idol - Star (4.47) / Bier (1.47)
26. Krug - Bier (4.47) / Star (1.33)
27. Neid - Hass (4.60) / Tanz (1.67)
28. Ball - Tanz (4.60) / Hass (1.40)
29. Dame - Frau (4.87) / Wald (1.80)
30. Baum - Wald (4.67) / Frau (1.60)
31. Sekt - Wein (4.60) / Kanu (1.13)
32. Boot - Kanu (4.73) / Wein (2.13)
33. Herd - Topf (4.47) / Gang (1.53)
34. Flur - Gang (4.67) / Topf (1.53)
35. Saal - Raum (4.47) / Mann (1.60)
36. Herr - Mann (4.80) / Raum (1.60)
37. Nerv - Hirn (4.67) / Welt (1.80)
38. Erde - Welt (4.60) / Hirn (1.60)
39. Kern - Nuss (4.33) / Lärm (1.27)
40. Hupe - Lärm (3.87) / Nuss (1.13)
41. Auto - Taxi (4.67) / Ruhe (1.87)
42. Muße - Ruhe (4.33) / Taxi (1.40)
43. Sieb - Loch (4.07) / Kind (1.53)
44. Baby - Kind (4.53) / Loch (1.40)
45. Brut - Nest (4.40) / Glas (1.60)
46. Vase - Glas (4.33) / Nest (1.53)
47. Horn - Jagd (4.27) / Wand (1.73)
48. Putz - Wand (4.20) / Jagd (1.27)
49. Helm - Kopf (4.13) / Text (1.07)
50. Satz - Text (4.20) / Kopf (1.80)
51. Korb - Obst (4.07) / Nase (1.27)
52. Auge - Nase (4.20) / Obst (1.60)
53. Land - Feld (4.07) / Bein (1.60)
54. Knie - Bein (4.53) / Feld (1.60)
55. Eile - Hast (4.73) / Dank (1.93)
56. Lohn - Dank (4.13) / Hast (1.73)
57. Hand - Ring (4.27) / Park (2.07)
58. Bank - Park (4.60) / Ring (1.73)
59. Urne - Sarg (4.47) / Buch (1.67)
60. Wort - Buch (4.20) / Sarg (2.00)
61. Wahl - Jury (4.00) / Lust (2.07)
62. Gier - Lust (4.40) / Jury (1.53)

Five letters (118)

63. Narbe - Wunde (4.73) / Bohne (1.07)
64. Erbse - Bohne (4.60) / Wunde (1.13)
65. Niere - Leber (4.60) / Moral (1.20)
66. Ethik - Moral (4.67) / Leber (1.20)
67. Depot - Lager (4.87) / Suppe (1.33)
68. Kelle - Suppe (4.60) / Lager (1.33)
69. Kakao - Milch (4.60) / Anzug (1.40)
70. Jacke - Anzug (4.60) / Milch (1.07)
71. Probe - Übung (4.40) / Tulpe (1.13)
72. Nelke - Tulpe (4.47) / Übung (1.00)
73. Kutte - Mönch (4.53) / Feuer (1.33)
74. Brand - Feuer (4.67) / Mönch (1.20)
75. Bluse - Ärmel (4.47) / Organ (1.20)
76. Lunge - Organ (4.67) / Ärmel (1.33)
77. Decke - Stuck (4.47) / Krieg (1.27)
78. Bombe - Krieg (4.53) / Stuck (1.13)
79. Möbel - Regal (4.60) / Küste (1.60)
80. Bucht - Küste (4.67) / Regal (1.07)
81. Karre - Wagen (4.60) / Braut (1.40)
82. Kleid - Braut (4.67) / Wagen (1.27)
83. Beton - Stahl (4.20) / Nebel (1.27)
84. Dunst - Nebel (4.87) / Stahl (1.20)
85. Hecke - Busch (4.53) / Lippe (1.20)
86. Stift - Lippe (4.33) / Busch (1.13)
87. Kamin - Asche (4.40) / Blüte (1.13)
88. Honig - Blüte (4.47) / Asche (1.20)
89. Kerze - Docht (4.67) / Salat (1.27)
90. Blatt - Salat (4.60) / Docht (1.47)
91. Druck - Zwang (4.27) / Tanne (1.27)
92. Buche - Tanne (4.67) / Zwang (1.13)
93. Stiel - Blume (4.40) / Mütze (1.07)
94. Schal - Mütze (4.47) / Blume (1.33)
95. Lotto - Glück (4.53) / Fluss (1.07)
96. Teich - Fluss (4.67) / Glück (1.67)
97. Orkan - Sturm (4.73) / Junge (1.73)
98. Knabe - Junge (4.87) / Sturm (1.40)
99. Haken - Angel (4.53) / Sport (1.40)
100. Halle - Sport (4.60) / Angel (1.40)
101. Möhre - Gurke (4.47) / Sucht (1.47)
102. Droge - Sucht (4.73) / Gurke (1.40)
103. Hitze - Wärme (4.80) / Folge (1.93)
104. Serie - Folge (4.93) / Wärme (1.47)
105. Tisch - Stuhl (4.53) / Ärger (1.33)
106. Frust - Ärger (4.73) / Stuhl (1.60)
107. Bitte - Gebet (4.13) / Maler (1.27)
108. Farbe - Maler (4.67) / Gebet (1.27)
109. Palme - Insel (4.40) / Sahne (1.47)
110. Torte - Sahne (4.60) / Insel (1.27)
111. Luxus - Yacht (4.47) / Nadel (1.33)
112. Stich - Nadel (4.20) / Yacht (1.13)
113. Stoff - Faser (4.67) / Hotel (1.47)
114. Suite - Hotel (4.47) / Faser (1.53)
115. Acker - Bauer (4.53) / Bogen (1.67)
116. Pfeil - Bogen (4.80) / Bauer (1.53)
117. Wolke - Regen (4.67) / Birne (1.07)
118. Apfel - Birne (4.60) / Regen (2.13)
119. Boden - Grund (4.60) / Griff (1.67)
120. Knauf - Griff (4.33) / Grund (1.20)
121. Punkt - Komma (4.67) / Eisen (1.47)
122. Nagel - Eisen (4.40) / Komma (1.60)
123. Milde - Gnade (4.53) / Linie (1.53)
124. Zeile - Linie (4.27) / Gnade (1.27)
125. Stolz - Würde (4.67) / Leder (1.53)
126. Schuh - Leder (4.33) / Würde (1.53)
127. Glanz - Chrom (4.20) / Stamm (1.87)
128. Rinde - Stamm (4.73) / Chrom (1.13)
129. Feger - Besen (4.60) / Kiosk (1.33)
130. Stand - Kiosk (4.20) / Besen (1.53)
131. Grill - Wurst (4.53) / Nacht (2.20)
132. Stern - Nacht (4.60) / Wurst (1.07)
133. Angst - Sorge (4.87) / Party (1.80)
134. Feier - Party (4.93) / Sorge (2.13)
135. Sitte - Regel (4.07) / Taste (1.13)
136. Knopf - Taste (4.60) / Regel (1.73)
137. Krone - Prinz (4.33) / Geige (1.33)
138. Cello - Geige (4.60) / Prinz (1.80)
139. Knast - Zelle (4.53) / Wiese (1.20)
140. Rasen - Wiese (4.27) / Zelle (1.87)
141. Ferse - Hacke (4.00) / Dauer (1.20)
142. Länge - Dauer (4.60) / Hacke (1.67)
143. Perle - Kugel (3.87) / Eiche (1.20)
144. Ahorn - Eiche (4.60) / Kugel (1.53)
145. Kniff - Trick (4.47) / Bauch (2.00)
146. Magen - Bauch (4.60) / Trick (1.40)
147. Pirat - Säbel (4.40) / Staub (1.47)
148. Dreck - Staub (4.47) / Säbel (1.73)
149. Atlas - Karte (4.67) / Licht (1.47)
150. Sonne - Licht (4.60) / Karte (2.20)
151. Spiel - Pokal (4.40) / Kabel (1.67)
152. Draht - Kabel (4.40) / Pokal (1.53)
153. Wanne - Eimer (4.00) / Brief (1.07)
154. Paket - Brief (4.33) / Eimer (1.80)
155. Marke - Porto (3.80) / Alter (1.73)
156. Greis - Alter (4.60) / Porto (1.20)
157. Qualm - Rauch (5.00) / Agent (2.13)
158. Spion - Agent (4.47) / Rauch (1.87)
159. Elend - Armut (4.87) / Radio (1.93)
160. Musik - Radio (4.60) / Armut (2.13)
161. Bühne - Szene (4.53) / Zange (1.73)
162. Feile - Zange (3.80) / Szene (1.20)
163. Trieb - Zweig (3.93) / Grube (1.13)
164. Senke - Grube (3.93) / Zweig (1.33)
165. Weite - Größe (4.33) / Haube (1.33)
166. Kappe - Haube (4.00) / Größe (1.67)
167. Thron - König (4.53) / Eifer (2.00)
168. Fleiß - Eifer (4.60) / König (2.07)
169. Faden - Leine (4.13) / Reise (1.47)
170. Fahrt - Reise (4.67) / Leine (2.33)
171. Harfe - Engel (3.93) / Lücke (1.80)
172. Spalt - Lücke (4.33) / Engel (1.53)
173. Hülle - Folie (4.07) / Seife (1.73)
174. Blase - Seife (4.40) / Folie (1.87)
175. Anker - Hafen (4.27) / Strom (1.80)
176. Blitz - Strom (4.47) / Hafen (2.07)
177. Truhe - Kiste (4.73) / Kanne (2.00)
178. Tasse - Kanne (4.40) / Kiste (2.33)
179. Koran - Bibel (4.73) / Stein (1.93)
180. Mauer - Stein (4.33) / Bibel (2.40)

Six letters (80)

181. Gemüse - Tomate (4.73) / Metall (1.13)

182. Silber - Metall (4.33) / Tomate (1.07)
183. Kachel - Fliese (4.60) / Melone (1.07)
184. Ananas - Melone (4.47) / Fliese (1.20)
185. Käufer - Handel (4.47) / Schnee (1.33)
186. Flocke - Schnee (4.87) / Handel (1.27)
187. Diesel - Benzin (4.73) / Eskimo (1.07)
188. Arktis - Eskimo (4.47) / Benzin (1.40)
189. Tropen - Urwald (4.60) / Rummel (1.40)
190. Kirmes - Rummel (4.87) / Urwald (1.40)
191. Hopfen - Gerste (4.67) / Format (1.13)
192. Rahmen - Format (4.13) / Gerste (1.07)
193. Bonbon - Zucker (4.47) / Messer (1.27)
194. Klinge - Messer (4.60) / Zucker (1.20)
195. Gläser - Brille (4.67) / Steuer (1.13)
196. Abgabe - Steuer (4.40) / Brille (1.33)
197. Killer - Mörder (4.80) / Bäcker (1.60)
198. Kuchen - Bäcker (4.53) / Mörder (1.13)
199. Gesang - Stimme (4.67) / Kupfer (1.13)
200. Bronze - Kupfer (4.53) / Stimme (1.53)
201. Kittel - Doktor (4.40) / Anfang (1.20)
202. Beginn - Anfang (4.73) / Doktor (1.40)
203. Ferien - Urlaub (4.73) / Kanone (1.33)
204. Pulver - Kanone (4.47) / Urlaub (1.40)
205. Hefter - Ordner (4.67) / Soldat (1.20)
206. Gewehr - Soldat (4.60) / Ordner (1.67)
207. Sattel - Reiter (4.60) / Daumen (1.27)
208. Finger - Daumen (4.60) / Reiter (1.53)
209. Weiher - Tümpel (4.33) / Filter (1.20)
210. Kaffee - Filter (4.67) / Tümpel (1.47)
211. Felsen - Klippe (4.67) / Becher (1.13)
212. Schale - Becher (4.00) / Klippe (1.27)
213. Herbst - Sommer (4.33) / Profit (1.20)
214. Gewinn - Profit (4.80) / Sommer (1.73)
215. Pommes - Imbiss (4.73) / Anhang (1.13)
216. Zusatz - Anhang (4.47) / Imbiss (1.87)
217. Husten - Grippe (4.40) / Leiter (1.20)
218. Treppe - Leiter (4.00) / Grippe (1.13)
219. Becken - Wasser (4.33) / Puzzle (1.40)
220. Rätsel - Puzzle (4.47) / Wasser (1.33)
221. Infekt - Fieber (4.33) / Schiff (1.67)
222. Kutter - Schiff (4.60) / Fieber (1.27)
223. Stelle - Posten (4.13) / Tumult (1.53)
224. Unruhe - Tumult (4.73) / Posten (1.33)
225. Pappel - Fichte (4.47) / Rücken (1.13)
226. Wirbel - Rücken (3.87) / Fichte (1.27)
227. Tusche - Wimper (4.53) / Kosten (1.53)
228. Spesen - Kosten (4.07) / Wimper (1.20)
229. Kiefer - Gebiss (3.67) / Furcht (1.33)
230. Bammel - Furcht (4.87) / Gebiss (1.40)
231. Schema - Modell (4.60) / Risiko (2.00)
232. Wagnis - Risiko (4.73) / Modell (1.53)
233. Planet - Rakete (4.00) / Banane (1.27)
234. Frucht - Banane (4.20) / Rakete (1.20)
235. Chemie - Physik (4.67) / Teufel (1.87)
236. Hörner - Teufel (4.27) / Physik (1.40)
237. Jurist - Anwalt (4.87) / Statue (1.93)
238. Museum - Statue (4.13) / Anwalt (1.53)
239. Götter - Tempel (4.47) / Umfang (1.80)
240. Ausmaß - Umfang (4.60) / Tempel (1.80)
241. Beutel - Tasche (4.47) / Spitze (1.80)
242. Gipfel - Spitze (4.07) / Tasche (1.27)
243. Wurzel - Knospe (4.20) / Ritual (2.33)
244. Brauch - Ritual (4.93) / Knospe (1.40)
245. Ausweg - Lösung (4.60) / Träger (1.40)
246. Stütze - Träger (4.07) / Lösung (1.93)
247. Kummer - Trauer (5.00) / Marine (1.93)
248. Flotte - Marine (4.40) / Trauer (2.13)
249. Muskel - Athlet (4.47) / Wecker (1.40)
250. Morgen - Wecker (4.47) / Athlet (2.27)
251. Blende - Kamera (4.47) / Gewalt (1.80)
252. Waffen - Gewalt (4.60) / Kamera (2.13)
253. Nation - Flagge (4.33) / Folter (2.13)
254. Tortur - Folter (4.20) / Flagge (1.33)
255. Galgen - Henker (4.67) / Fehler (2.40)
256. Irrtum - Fehler (4.87) / Henker (2.07)
257. Talent - Stärke (3.93) / Gebiet (2.20)
258. Fläche - Gebiet (4.53) / Stärke (1.67)
259. Gruppe - Partei (4.27) / Straße (2.27)
260. Häuser - Straße (4.20) / Partei (2.33)

Seven letters (52)

261. Meldung - Bericht (4.87) / Getränk (1.47)
262. Flasche - Getränk (4.67) / Bericht (1.20)
263. Mission - Auftrag (4.80) / Alkohol (1.40)
264. Schnaps - Alkohol (4.47) / Auftrag (1.13)
265. Anstieg - Zunahme (4.67) / Polizei (1.53)
266. Gendarm - Polizei (4.73) / Zunahme (1.20)
267. Fransen - Teppich (4.40) / Anzeige (1.20)
268. Inserat - Anzeige (4.80) / Teppich (1.40)
269. Prüfung - Klausur (4.93) / Werbung (1.93)
270. Reklame - Werbung (5.00) / Klausur (1.40)
271. Applaus - Beifall (4.93) / Seemann (1.40)
272. Matrose - Seemann (4.80) / Beifall (1.73)
273. Spritze - Impfung (4.40) / Aufruhr (1.27)
274. Krawall - Aufruhr (4.80) / Impfung (1.40)
275. Skelett - Knochen (4.67) / Abstand (1.60)
276. Distanz - Abstand (4.87) / Knochen (1.47)
277. Apparat - Telefon (4.67) / Schwert (1.67)
278. Rüstung - Schwert (4.47) / Telefon (1.07)
279. Zuhause - Wohnung (4.73) / Absicht (1.60)
280. Vorsatz - Absicht (4.73) / Wohnung (1.53)
281. Ballade - Gedicht (4.47) / Pudding (1.07)
282. Dessert - Pudding (4.67) / Gedicht (1.73)
283. Bandage - Verband (4.73) / Ankunft (1.20)
284. Empfang - Ankunft (4.33) / Verband (1.60)
285. Ausrede - Vorwand (4.47) / Vorhang (1.47)
286. Gardine - Vorhang (4.87) / Vorwand (1.87)
287. Premier - Kanzler (4.13) / Brunnen (1.13)
288. Fontäne - Brunnen (4.13) / Kanzler (1.27)
289. Edition - Ausgabe (4.60) / Gedanke (1.60)
290. Einfall - Gedanke (4.47) / Ausgabe (1.60)
291. Anklage - Vorwurf (4.60) / Merkmal (1.73)
292. Symptom - Merkmal (4.47) / Vorwurf(1.60)
293. Blamage - Skandal (4.13) / Eingang (1.40)
294. Öffnung - Eingang (4.60) / Skandal (1.73)
295. Schloss - Fahrrad (4.20) / Magazin (2.20)
296. Journal - Magazin (4.87) / Fahrrad (1.40)
297. Schwere - Gewicht (4.40) / Trainer (1.53)
298. Spieler - Trainer (4.53) / Gewicht (2.07)
299. Zeitung - Artikel (4.67) / Kleider (1.93)
300. Schrank - Kleider (4.67) / Artikel (2.07)
301. Sektion - Bereich (4.40) / Richter (1.80)

302. Prozess - Richter (4.47) / Bereich (1.87)
303. Fassung - Version (4.73) / Meister (2.07)
304. Experte - Meister (4.93) / Version (2.47)
305. Vorsitz - Leitung (4.40) / Theater (2.00)
306. Kulisse - Theater (4.53) / Leitung (1.87)
307. Dynamik - Energie (4.53) / Pflanze (2.40)
308. Gärtner - Pflanze (4.53) / Energie (1.87)
309. Gemälde - Malerei (4.67) / Fenster (2.40)
310. Scheibe - Fenster (4.73) / Malerei (2.27)
311. Gerücht - Legende (3.67) / Papiere (1.87)
312. Ausweis - Papiere (4.67) / Legende (2.13)

Animal names (60)

Adler, Amsel, Barsch, Biene, Bison, Eber, Elster, Eule, Falter, Fasan, Fliege, Floh, Frosch, Fuchs, Gepard, Grille, Hahn, Hammel, Hecht, Hering, Hummer, Hyäne, Igel, Iltis, Kakadu, Kalb, Kauz, Kobra, Krake, Kröte, Lama, Lamm, Laus, Luchs, Mammut, Marder, Meise, Ochse, Pfau, Pudel, Puma, Python, Ratte, Reiher, Robbe, Rochen, Schabe, Schaf, Schwan, Spinne, Taube, Tiger, Wanze, Wels, Wespe, Wiesel, Wisent, Wolf, Wurm, Zander

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Arbeit selbstständig und ohne unerlaubte Hilfe verfasst habe, dass ich die Dissertation an keiner anderen Universität eingereicht habe und keinen Doktorgrad in dem Promotionsfach Psychologie besitze, und dass mir die zugrunde liegende Promotionsordnung der Mathematisch-Naturwissenschaftlichen Fakultät II der Humboldt Universität vom 3. August 2006 bekannt ist.

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